ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. I April, 1915 No. 4

PUBLISHED UNDER THE
AUSPICES OF THE GRADUATE SCHOOL BY
THE UNIVERSITY OF ILLINOIS

SOME NORTH AMERICAN LARVAL TREMATODES

WITH EIGHT PLATES

BY

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Contributions from the
Zoological Laboratory of the University of Illinois under the direction of
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THESIS

Submitted in Partial Fulfilment of the Requirements
for the Degree of Doctor of Philosophy
in Zoology in the Graduate School
of the University of Illinois
1914

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INTRODUCTION

Practically nothing is known of the life-histories of the trematodes of North America. Even in Europe where many new adults are being described each year only a few developmental cycles are completely known. One reason for this is to be found in the difficulties involved.

Two methods of attacking trematode life-history problems have been employed. One is to attempt to prove specific identity between cercariae and adults by structural comparisons, and the other is to attempt to find the relationship experimentally. Positive results from the first method have been few. The structure of certain types of cercariae gives no suggestion of the family to which the adult belongs, and in the more differentiated forms generic identification is very rarely possible. Even when the comparison is narrowed to very similar cercariae and adults from limited localities it is safest to consider the results as merely suggestive. Many errors have crept into the literature from too much reliance on this method. In some cases the mere suggestion of probable identity by one author has been taken by another as if it were an established fact. It is only when the adult has been experimentally raised from the cercariae or the larvae from the eggs of the adult that the establishment of specific identity can be made sure. The experimental method of study also has its dangers. The factors involved are so complex and so little understood that only the most carefully controlled experiments can be considered as conclusive. In some very recent work as well as in older papers larvae and adults, shown later to be entirely unrelated, have been joined experimentally.

In connection with efforts to solve developmental problems it is often argued that given the structure of a cercaria, it is possible to draw conclusions as to the environment where it encysts, the life it leads, etc. Further, that if the course of development of one member of a group is known, it can be concluded that the others follow the same lines. Dollfus (1914) finds evidence against both generalizations. He states that after a comparative examination of cercariae and the environment in which they live, he can assert that cercariae very similar in structure dwell in different hosts and have very different kinds of development, and that cercariae very different morphologically live

in identical environments and have similar courses of development. Certainly in the study of the development of digenetic trematodes it will be necessary to increase very greatly the number of particular instances known before the induction of general principles can safely go very far.

In Europe, where more is known of trematode development than elsewhere, the foundations of this study were laid in the middle of the last century by the work of such men as Leuckart, Wagener, Pagenstecker, La Valette St. George, de Filippi, and Moulinié. Altho they made but little progress in the actual working out of developmental cycles, their descriptions of large numbers of cercariae from molluscs have formed the basis for later work. In England Nicoll and Marie Lebour have very recently made some headway in the study of larval trematodes altho as yet little experimental work has been done. In North America only a beginning has been made in the study of adult trematodes and as yet there are only a very few scattered observations of larval stages. The present work was undertaken by the writer at the suggestion of Professor Henry B. Ward as an attempt to open up this almost untouched field in North America.

Most of the descriptions of larval trematodes from North American molluscs are very inadequate and in many cases it is impossible to tell to which general group of cercariae the forms belong. In only a very few instances are either drawings or measurements given. The following list is an attempt to bring together all references to date on larval trematodes from North American molluscs.

1. *Cercaria hyalocauda Haldeman* (date?) also reported by Evarts (1880). Host *Physa heterostropha* Say. Locality (?).

2. *Cercaria bilineata* Haldeman (1840). Host *Limnea catascopium,* Camden, Delaware.

3. *Cercariaeum vagens* (Leidy) (1847: 220-221)
Syn. *Distoma helicis* (Leidy 1847:220-221)
" *pericardium* Creplin (1849)
" *vagens* Leidy (1850: 304-310)
Cercariaeum helicis alternatae Diesing (1855:398)
398)
" *vagens* Diesing (1858:42)
Host *Helix alternata* and *Helix albolabris,* Philadelphia, Pa.

4. *Cercaria agilis* Leidy (1858: 110). Found free in the Delaware river.

5. *Monostoma (Glenocercaria) lucania* Leidy (1877:200-201)
Host *Planorbis parvus.* Philadelphia, Pa.

6. *Distoma (Gymnocephala) ascoidea* Leidy (1877:201). Host, *Planorbis parvus*, Philadelphia, Pa.

7. *Distoma centrappendiculatum* Leidy (1890:416).
Syn., *Distoma appendiculatum* Leidy (1877:202).
Host, *Helix arbora*, Philadelphia, Pa.

8. *Distoma cornifrons* Leidy (1878:382-383). Host, *Donax fosser*, Cape May, New Jersey.

9. *Distoma lasium* Leidy (1890). Host, *Ilyanassa obsoleta*, Beach Haven, New Jersey.

10. *Cercaria platyura* Leidy (1890:415-416). Free in a pool at Fort Bridger, Wyoming.

11. Cercaria of *Diplodiscus temporatus* Stafford, Cary (1909). Host, *Goniobasis virginica*, Princeton, New Jersey.

The present paper adds fourteen new species of cercariae from North American fresh-water snails. A preliminary report, taking up briefly the structure and activity of these cercariae has already been published (Cort, 1914).

METHODS OF STUDY

To obtain this material examinations were made of large numbers of snails from various localities. I want to express my thanks to Dr. Ruth Marshall, Dr. M. F. Guyer, Dr. G. R. La Rue, Dr. B. M. Allen, Dr. F. W. Carpenter, Dr. H. S. Pratt, Mr. A. F. Coutant, Mr. Hermann Douthitt, Dr. C. S. Mead, Dr. A. Richards, Dr. C. C. Nutting, and Dr. J. E. Ackert for their kindness in collecting and shipping me living snails. Without their aid it would have been impossible to have obtained the material for this study.

To Professor Henry B. Ward, under whose direction this work has been carried on, I wish to express my appreciation for his interest and helpful suggestions.

The following method was employed in the examination of snails for larval trematodes. The shell was cut or crushed so as to remove the body, if possible, unbroken. An examination was then made with the low power of the microscope. If larval trematodes were present, some of them were almost invariably loosened from the infected part and scattered around the snail in the water. The digestive gland was the organ most usually infected, its color being often changed by the pigmentation of the sporocysts or rediae. When infection was found a part of the diseased tissue was preserved whole for sectioning, an-

other portion was teased apart to free the larvae for preserving for toto mounts, and the remainder was used for the study of the living animals. Much of the anatomy of the cercariae could be made out from living specimens. In fact this proved to be an extremely important part of the study, since some points, for example the smaller branches of the excretory system and the movement, could only be observed in this manner.

For preservation of material a number of fixatives were used. In fixing the freed cercariae for toto mounts the best results were obtained by the use of hot solutions of Bouin's picro-aceto-formol or corrosive-acetic. For sectioning the infected organs were fixed in toto, since as suggested by Cary (1909:597) this is easier and gives better results than attempting to section freed individuals. A corrosive-acetic solution was ordinarily used for fixing this material. Rediae and cercariae for toto mounts were stained in Mayer's haemalum, Delafield's haematoxylin, Conklin's picro-haematoxylin, and Mayer's paracarmine. The specimens were as a rule considerably overstained in dilute solutions of the stain and differentiated in HCl_2 under the microscope. In mounting it was found convenient to place large numbers of the larvae on one slide. The infected organs to be sectioned were usually stained in bulk in Ehrlich's acid haematoxylin, cut into sections 5 to 7 micra in thickness, and differentiated on the slide, part of them being counterstained in eosin.

On account of their great mobility, small size, and remarkable power of changing their shapes, some cercariae are very difficult objects to study. No very accurate measurements can be made of living specimens, and in preserved material they are often contracted and distorted. With the living cercariae an attempt was made to get the range of variability, and in preserved material, whenever possible, the average measurements of a number of well extended specimens were taken. The measurements of preserved material are less than those from living specimens of the same kind, even the suckers shrinking perceptibly after preservation. For these reasons comparisons of the cercariae based on size and shape, as Lühe (1909:173) has suggested, are not always by themselves very reliable criteria for specific determination.

MONOSTOME CERCARIAE

About five per cent., of the largest specimens of *Physa gyrina* from a drainage ditch north of Urbana, Illinois, examined in December, 1913, were infected with the rediae and cercariae of a monostome. I propose to name this species *Cercaria urbanensis.* The infection was in the liver of the snail and there were present both rediae in different stages of development and free cercariae. No sporocysts were found and none of the rediae contained rediae. It is interesting to note that in the descriptions of monostome larvae no mention is made of sporocysts, and only one observation of rediae developing from rediae. Braun (1892:805-806) notes that in certain of the monostomes rediae are already developing in the free swimming miracidia, which he considers to already represent sporocysts. Looss (1896:197) states that in material of *Cercaria imbricata* Looss collected from *Bythinia tentaculata* near Leipzig, rediae were present in which rediae were developing. From this he concludes that the life-history of this species is accomplished in the same manner as that of the amphistomes, which have several generations of rediae.

When freed from the liver of the snail the redia had considerable power of extension and contraction. The immature ones especially stretched out the anterior end and reached in all directions. No locomotor appendages were present either in young or mature redia and no locomotion was noted. In fact the redia of *Cercaria imbricata* Looss is the only monostome redia that is reported with locomotor appendages. According to Looss (1896:196) the appendages in this species were well marked in the young redia but more or less effaced with advancing age. In some of the largest rediae of *Cercaria urbanensis* very peculiar annular constrictions were noted in different parts of the body, which divided it into two or three separate regions connected by very narrow passages (Fig. 12). These constrictions seem to be due to temporary unequal contraction states in different regions of the circular body muscles. This condition for the redia of *Cercaria urbanensis* was observed only in preserved material. Leidy (1877:200; 1904:143-144) notes such constrictions in the living redia of a monostome cercaria which he calls *Monostoma lucanica.*

The methods of locomotion of *Cercaria urbanensis,* either when swimming in open water or when upon a substratum, are very striking. The body when swimming was contracted almost into a round ball and the tail, which was curled ventrally so that it passed across the ventral surface of the body, lashed backward and forward with great rapidity. This method of locomotion was very effective and the cercariae could be seen even with the naked eye in rapid movement thru the water. In spite of the lack of a ventral sucker the cercaria was able to move well on a surface by utilizing two projections which form the posterior lateral angles of the body. In the process of locomotion the cercaria took hold with its oral sucker and the body contracted until it was practically round. Then the sucker let go its hold and the body stretched out, at the same time extending the posterior projections until they became little points digging into the substratum. Again the oral sucker took hold and again the body contracted. By a continued repetition of these movements this cercaria progressed at about the same rate of speed as those having two suckers. After each contraction the posterior projections held the amount gained. During the contraction and at the beginning of the extension of the body the tail kept lashing very rapidly, but during the rest of the movement it was held still and somewhat contracted.

Some of the freed cercariae after moving around for a while settled down and formed cysts. A cercaria which was moving along on a surface extended and contracted its body more and more slowly, until while retaining a hold with the oral sucker the body became almost round. While in this position the cystogenous material was extruded, and the appearance was soon given of a round cyst with a tail attached. Soon the worm inside freed itself from its connection with the tail and squirmed around in the cyst. Finally the tail wriggled loose from the cyst and continued swimming around for considerable time, resembling in form and movement a free living nematode. The cysts formed in a watch glass were flattened on the lower surface and had much the shape of a chocolate drop. The process of encystment is illustrated by figures 1, 2, 3, and 4. Encystment in the open has been noted for *Cercaria ephemera* Nitzch. The encystment of this species, which was first reported by Nitzch (1807), was the first described for a cercaria. La Valette St. George (1855:33-34) described and figured the process for the same species, and in one of his figures shows the tail attached to the cyst. Von Linstow (1896:377) for *Cercaria monistomi* von Linstow describes the encystment in the same host as the larval generation.

The rediae of *Cercaria urbanensis* (Figs. 10, 11, and 14) were in various stages of development, varying in length from 0.52 mm. to 1.08 mm. and in width from 0.12 mm. to 0.22 mm. In shape they are elongate sac-like forms smallest at the anterior and widest a short distance in front of the posterior extremity. The mouth is at the anterior tip and the pharynx varies with the size of the animal. In the smallest redia studied which had a length of 0.52 mm. the pharynx was 0.038 mm. in length by 0.048 mm. in width while in one 1.08 mm. in length it was 0.07 mm. by 0.08 mm. The passage thru the pharynx immediately opens into the intestine which is at first narrow but soon widens greatly. In all stages of development the intestine is proportionally very large, having a diameter of from one-third to two-thirds the width of the body and reaching to within 0.08 mm. to 0.16 mm. of the posterior end. It is rather clear and transparent and contains only a small amount of food material floating in a considerable quantity of fluid. The outer cuticula of the redia is very thin and can hardly be distinguished as a separate layer. Inside of this is a very strong layer of circular muscles which encircle the body as separate strands, each about 0.0018 mm. in width and about the same distance apart. The strands of the longitudinal layer are very thin and only visible under favorable conditions. Inside of the muscle layers are several rows of parenchymatous cells with rather large nuclei. These cells do not form a circumscribed lining of the body cavity but are irregular and in young rediae where the lining is several cells thick, strands extend from them thruout the body cavity forming an irregular network (Fig. 13). Into this loosely filled space between the body wall and the intestine the cercariae push. In the oldest rediae the wall has been reduced to one layer and the movements of the cercariae have broken down the parenchymatous strands and converted the region between the wall and the intestine into a well defined cavity, which is more or less completely filled with developing cercariae. In the posterior end of the redia is the germ gland, in front of this are germ balls and further forward in the older rediae are differentiated cercariae. In the youngest redia (Fig. 10) studied the developing embryos were all back of the middle of the body and the furtherest developed was a mass of embyronic cells about 0.09 mm. in length and 0.06 in width and having no tail. In none of the rediae was the body cavity crowded with cercariae, there being but two or three well developed forms, and in one mature specimen there were no differentiated cercariae present leaving the body cavity empty for about two-thirds of its length. These conditions and the fact that the oldest cercariae in the rediae are not fully mature and that matured and almost matured cercariae are found

free in the livers of the infected snails, show that the cercariae as they develop are continually making their way out of the rediae to finish their growth in the liver of their host. The most highly differentiated cercaria found in the redia (Fig. 11, 14, cr) was 0.3. mm. in length and 0.1 mm. in width and had a tail 0.22 mm. in length. The two lateral eye-spots were developed and the pigment was present to a considerable extent around them, but was not further scattered or concentrated to form the so-called intermediate eye-spot. Outlines of the longitudinal vessels of the excretory system and the anlage of the reproductive system could be clearly distinguished. The oral sucker was well defined but none of the rest of the digestive system could be distinguished.

The mature *Cercaria urbanensis* (Fig. 5) varies greatly in shape being at greatest contraction nearly round, about 0.27 mm. in length and 0.20 mm. in width and when extended 0.54 mm. long and 0.11 mm. wide. When not in motion the tail is contracted being about 0.2 mm. long and 0.05 mm. wide at its base. At times of greatest movement the tail becomes attenuated to about one-half its usual diameter and often reaches a length of 1.2 mm. It is weakly attached to the dorsal mid-line of the posterior end of the body and tapers to a sharp point. There is an inverse ratio between the contraction of the body and the tail for when the body is most contracted the tail is most extended and vice versa.

In view of the great power of movement of *Cercaria urbanensis* the histological structure of its tail is of considerable interest. Just inside of the thin cuticula is a layer of circular muscles arranged as strands separated by about twice their length from each other. Inside of this is a very strong layer of longitudinal muscle fibers each 0.0026 mm. in diameter. Next comes a single layer of parenchymatous cells somewhat irregularly elongated with nuclei 0.005 mm. in diameter. Extending the length of the tail and forming a core are two rows of long cells which are close together and have their long axes parallel with the length of the tail. These cells vary in size having a length from 0.028 mm. to 0.035 mm. In a cross section of a tail 0.075 mm. wide one of these cells measured 0.026 mm. in thickness and 0.014 mm. in width. They are full of heavily staining granules and their nuclei are 0.007 mm. in diameter. There is nothing suggestive of a possible function for these cells. Figure 9, a cross section thru a tail, shows the structures described above.

At the posterior lateral angles of the body are projections which may be extended to aid the animal in locomotion. The tips of these projections are made firm by structures which appear to be infoldings

of the outer cuticula. One of the structures (Fig. 8) is ovoid with two cuticular walls, having a loosely fitted space between them, and a very narrow central cavity communicating with the exterior by a small pore at the tip of the projection. They apparently have no sucking action, since no muscles are present and the central cavity contracts when the projection is extended. They evidently have a function in locomotion analogous to setae. Similar locomotor projections have been described for *Cercaria ephemera* Nitzch and *Cercaria imbricata* Looss, and for Leidy's (1877 :200) (1904 :143-144) *Monostoma lucania* from North America they are merely mentioned as conical projections. Ssinitzin (1905, Plate 4, figs. 75 and 76) figures these structures in *Cercaria ephemera* Nitzch as clearly circumscribed projections with a considerable cavity lined with spines. Figures 6a and b are copies of his figures. Certainly the structures figured by Ssinitzin differ considerably from those of *Cercaria urbanensis.* Marie Lebour (1907 :442) in the monostome cercaria from *Paludestrina stagnalis* which she considers to be *Cercaria ephemera* describes the posterior locomotor projections as sucker like structures, which are circular in outline and divided in two by a bar. Her figure shows them as structures quite comparable to those of *Cercaria urbanensis* but very different from Ssinitzin's figures. She assigns no especial reason for considering them to be sucking structures. The posterior locomotor projections as described by Looss (1896 :194) for *Cercaria imbricata* offer still greater differences. The cavity is comparatively large with but one cuticular wall and divided at its center into two parts by a projection. Figure 7 is a copy of Looss', Plate 14, Figure 151.

Mature specimens of *Cercaria urbanensis* are heavily pigmented especially at the anterior end, and have two lateral pigmented eyes with lenses and a central anterior spot which is formed by a condensation of pigment. The eyes are situated dorsad at each side of the large esophageal commissure and above the obtuse angles formed by the large nerves which pass forward and backward. Each true eye is formed by a mass of pigment in the form of a cup the bottom of which is thicker than the sides. A lens fits into the opening of the cup, leaving a space between its lower surface and the bottom of the cup. An eye spot has a diameter 0.017 mm. and the depth of the pigment cup is 0.024 mm. At the anterior end surrounding each eye are scattered pigment granules extending in all directions and about as clearly defined ventrally as dorsally. Anteriorly a condensation forms the so-called anterior eye spot, and scattered granules reach well beyond the limit of the oral sucker. Posteriorly the pigment granules become more

scattered and continue as two longitudinal lines to the posterior end of the body on each side of the excretory bladder (Fig. 5, p. 1). These lines of pigment extend thru the whole dorsal ventral thickness of the body and are as apparent on one side as on the other. Along each edge and appearing ventrally are two other irregular lines of pigment which do not extend as far back. Little pigment flecks are scattered from these lines out thru the body. In the young cercaria the pigment develops first around the eyespots in dense masses and spreads gradually with growth both forward and backward along the lines mentioned. It is only in the oldest cercaria that it is spread sufficiently to form the anterior spot and the lines extending to the posterior end.

The digestive system (Fig. 5) of *Cercaria urbanensis* is like that described for other monostome cercariae. The mouth at the anterior tip is sub-ventral and the oral cavity is surrounded by a relatively small oral sucker, averaging 0.043 mm. in length and 0.049 mm. in width. The esophagus is very narrow and 0.05 mm. to 0.06 mm. long depending on the contraction. The cecal bifurcations are close together at their beginnings but soon spread further apart. They are always within and slightly dorsad of the large longitudinal excretory vessels and extend almost to the end of the body. The ceca are not yet functional, being composed of a solid mass of cells.

The excretory system (Fig. 5, ex) is typical of the group. At the posterior end is the excretory bladder opening just below the base of the tail. From this extends forward two large vessels which unite in the midline just back of the oral sucker. Thruout their whole course they are filled with small round concretions which disappear in the process of preservation. It is very difficult to be positive of the relations of the excretory system of the tail but as nearly as they can be made out they are as follows: No openings could be found in the tail and a single vessel passed forward from near the tip becoming larger nearer the body and opening at the excretory pore.

Almost the whole body of *Cercaria urbanensis* is filled when mature with large unicellular cystogenous glands containing small granules. Only the very anterior tip, the posterior locomotor projections and the tail are free from them.

Only a few monostome cercariae have been recognized. All of these except *Cercaria lophocera* Filippi (1857:5) correspond very closely in structure to *Cercaria urbanensis*. *Cercaria imbricata* Looss is distinguished by the fact that the rediae have smaller intestines and lateral appendages and by the structure of the posterior locomotor projections of the cercaria (Looss 1896:192-197). Several different forms have

probably been described as *Cercaria ephemera* as it seems improbable that Ssinitzin and Lebour have described the same form. The only difference that can be definitely determined by comparing the descriptions of *Cercaria ephemera* with *Cercaria urbanensis* is in the structure of the posterior locomotor appendages of the cercaria. In von Linstow's (1896:376-377) description of *Cercaria monostomi* both rediae and cercariae are larger than in any of the other species, the arrangement of pigment is different from that in *Cercaria urbanensis,* and no posterior locomotor appendages are described. These may have been overlooked as they are very small and not easily seen unless the animal is studied alive. *Cercaria lophocera* described by Filippi (1857:5) from Italy is entirely different from all other monostomes known.

Two descriptions of monostome cercariae have been made from North America. Leidy (1877:200-201) describes as *Monostoma lucanica,* a form from *Planorbis parvus.* Unfortunately not enough detail is given to make the comparison possible. The other form is described by Haldeman as *Cercaria hyalocauda.* It has been impossible to find Haldeman's original description. Evarts (1880) describes this species from *Physa heterostropha.* Altho so little detail is given that a minute comparison cannot be made between this species and *Cercaria urbanensis,* certain points can be definitely made out. *Cercaria hyalocauda* is about half again as large as *Cercaria urbanensis,* and its cyst is much larger than that of the latter species, being 0.32 mm. to 0.20 mm. It seems evident that the two forms are not identical.

Altho monostome cercariae have been known since 1817, the life-history of no one of them has been proven experimentally. Looss (1896:-192-193) argues from distribution and structural correspondence that *Cercaria imbricata* from Egypt is the larval form of *Notocotyle triseriale* from the duck. Lühe (1909:178) suggests that *Cercaria ephemera* is the larval form of either *Notocotyle triseriale* or *Catatropis verrucosa* (Frol.), but cannot belong to *Typhlocoelum flavum* (Mehl.) on account of differences in the digestive systems of the two forms. So little is known of the monostomes of the United States that it is useless to generalize in regard to the life-history of *Cercaria urbanensis.*

AMPHISTOME CERCARIAE

Amphistome cercariae of two species were collected from specimens of *Planorbis trivolvis* from three localities. Two snails out of eighteen from Lawrence, Kansas had the livers infected with rediae and very large pigmented cercariae. Out of large numbers of *Planorbis trivolvis* examined from around Urbana, Illinois, one from a small pond

was infected with this same form. The second of these species, a smaller unpigmented cercaria, was found in one of twenty specimens of *Planorbis trivolvis* from a small pond in the suburbs of Chicago. In all the infected snails mature and immature cercariae were found free in the liver, the mature forms being nearest the periphery, and the active rediae contained no fully developed cercariae. There were no sporocysts present and no rediae in which rediae were developing, and in none of the infected snails were rediae or cercariae numerous. Since the large pigmented species is very unwieldy in movement, I propose to name it *Cercaria inhabilis,* and the smaller species on account of the way in which it changes its body shape will be given the name, *Cercaria diastropha.*

Cercaria inhabilis swam sluggishly in open water. It contracted its body and lashed its tail backward and forward, moving in an unwieldy, irregular fashion. In fact the body was too large in proportion to the size of the tail for rapid locomotion. On a substratum the cercaria extended and contracted the body but was unable to move by the aid of its suckers.

When in a state of average contraction, about that of figure 16, the body of *Cercaria inhabilis* is pear shaped, tapering in the anterior half, and wider but of uniform diameter posteriorly. It is the largest of the cercariae studied, having an average length in mounted specimens of 0.8 mm. and a width of 0.4 mm. The thickness is a little greater than half the width. The oral sucker is elongate, 0.16 mm. in length and 0.12 mm. in width with the retrodorsal pharyngeal pockets which are characteristic of some amphistomes. The acetabulum is very large averaging 0.23 mm. in diameter; it is at the posterior end of the body and is turned ventrad.

Two large eye-spots are present just back of the pharynx. They are located from one-fourth to one-third of the distance from the anterior to the posterior end, and in a specimen 0.27 mm. wide at this region, they were 0.065 mm. from the outer margins and 0.13 mm. apart. These eyes are composed of the lens and the cone of pigment like those already described for the monostome, *Cercaria urbanensis.* Figure 17, a section thru the eyes, shows them in their relation to the nervous system and other adjacent structures.

In the development of *Cercaria inhabilis* the pigment starts in the eyes and is deposited first in a peculiar way over most of the anterior half of the body. In the youngest cercariae found outside of the rediae very little pigment is seen and that found near the eyes (Fig. 18, p.). In forms a little older (Fig. 19, p.), the pigment has

begun to spread out a little forward and to the sides, but for the most part backward along two irregular lines. At first all the pigment strands were connected in an irregular way, but soon at the ends of the lines little flecks were scattered out. Backward along the lines the pigment becomes thicker (Fig. 20, p) and collects at points of union in the network masses. At an older stage, (Fig. 21, p) the pigment strands from the two lateral lines become connected and form an irregular network about the middle of the oral sucker, laterad as far as the sides, and backward to about the middle of the body. As the cercariae become older the masses and lines of pigment break up and are more scattered. In the mature specimen (Fig. 16) the pigmentation shows as scattered brownish flecks extending thru the whole thickness of the body (Fig. 17, p) and reaching from the oral sucker back to the middle.

The cystogenous glands in *Cercaria inhabilis* are as thickly developed dorsally as ventrally, and extend from the oral sucker to the acetabulum. Viewed from the surface they appear as small rounded bodies, 0.012 to 0.016 mm. in diameter, filled with rod-shaped cystogenous granules. Figure 17 shows them to be elongate, unicellular, club-shaped glands with small nuclei.

The tail of *Cercaria inhabilis* varies from one-third to greater than the body length. It is attached to the tip of the body above the acetabulum and is easly lost in free swimming animals. The cuticula of the tail is very thin and no trace could be found of circular muscles. The longitudinal muscle layer, however, is conspicuous and is formed of a series of strands each 0.0035 mm. in thickness, which extend from the base to the tip. Inside of the muscles is a layer of irregular parenchymatous cells, with nuclei 0.005 to 0.007 mm. in diameter, and irregular indistinct cell boundaries. The space between this layer and the excretory tubule, which courses down the center of the tail, is filled with large cells with faintly granular cytoplasm, and large nuclei, 0,008 to 0.009 mm. in diameter. These cells are similar to those forming the core of the tail of *Cercaria urbanensis,* but inclose no such darkly staining granules. Several of these cells may occur in one cross section since they do not seem to be arranged in regular rows. The central excretory tubule of the tail has a considerable diameter, and contains in its walls very large scattered nuclei, 0.01 to 0.012 mm. in diameter. A cross section of the tail (Fig. 22) shows these structures.

A comparison of the nucleoli of the different nuclei of the tail of *Cercaria inhabilis* is interesting. Of the three kinds of nuclei present viz. 1. nuclei of the excretory tubule, 2. nuclei of the large central cells, 3. parenchymatous nuclei, the first two have large very clearly defined nucleoli and little if any chromatin scattered outside of it. Of

these two the second is the larger. In the parenchymatous nuclei the nucleoli are quite small, not definite in outline, and much chromatin is scattered thru the nucleus.

The excretory vessel in the tail of *Cercaria inhabilis* is a large single tube running down almost to the tip, where it divides to open to each side (Fig. 16). This vessel becomes narrow as it passes from the tail to the body but immediately widens into the excretory bladder, which is a triangular vesicle dorsad and anteriad to the acetabulum. No vessels or flame cells were made out in the acetabulum. Into each corner of the bladder open vessels which were traced only as far as the eye-spots. In these vessels were present the round highly refractive concretions, already noted in the excretory system of *Cercaria urbanensis* and by Looss in the amphistome cercariae described by him (Looss, 1896:181).

The mouth of *Cercaria inhabilis* is at the anterior tip of the oral sucker which juts out slightly from the body. The anterior margin of the mouth cavity is smooth or only slightly roughened. There are no papillae present around the margin of the oral cavity such as Looss (1896:179) describes for the amphistome cercaria from Egypt, which he considers, to be the larva of *Gastrodiscus egyptiacus*. The mouth opens into an oral cavity, from which a narrow passage runs directly backword; this changes into the esophagus at the posterior limit of the oral sucker. Into each side of the oral cavity open the blind tubes of the retrodorsal pharyngeal pockets (Fig. 16, pp.). The oral cavity has a length of 0.059 mm. and the lateral blind tubes are 0.086 mm. in length. As it passes out of the oral sucker the digestive tube becomes the thin, straight-walled esophagus, 0.021 mm. in caliber, which has a length of 0.1 to 0.15 mm. depending on the state of contraction of the cercaria. Just before the esophagus bifurcates it is reinforced by a mass of circular muscle fibers of a sphincter, making a characteristic structure which superficially resmbles a pharynx. This pseudo-pharynx is about as long as wide, being 0.038 mm. in diameter, and has a wall 0.009 mm. thick, composed of from 12 to 14 separate layers of muscles. Longitudinal muscles were not made out either in this region or in the esophagus. The inner lining of the esophagus is non-cellular and tiny projections extend out into its lumen (Fig. 17, es). After bifurcation the intestinal ceca run laterally for a short distance and then turn posteriad to reach within 0.05 mm. to 0.06 mm. of the anterior margin of the acetabulum. The ceca are fairly wide, 0.028 mm. to 0.036 mm., and the inner walls contain flattened nuclei which jut out a little into their lumina. Figure 16 illustrates the relations of the digestive system.

In *Cercaria inhabilis* the anlage of the reproductive organs begins to take definite shape. It is composed of dense masses of small heavily staining nuclei. In the largest cercariae four areas connected by lines are marked out. At the middle line of the body just back of the bifurcation of the intestinal ceca, is an elongate mass which reaches up very close to the ventral surface. This is probably the anlage of the ends of the ducts of the reproductive system, leading up to the genital pore. Slightly back of this and close together are two masses, the primordia of the testes, and further back is the largest densest mass which represents the ovary and its surrounding structures (Fig. 16, ra).

Along with the cercariae in the livers of the infected snails were numbers of active radiae all in about the same stage of development (Fig. 15). When they were freed from the snail they were very mobile extending and contracting and making some progress even on the smooth surface of the watch glass. There were two pairs of locomotor appendages and the posterior extremity was attenuated and pointed. The anterior pair of locomotor appendages was just back of the posterior limit of the intestine and at normal extension the second pair was about the same distance back. The tail region was shorter and more slender. These proportions varied greatly with the contraction of the animal. In alcoholic material the locomotor appendages of the redia are often obliterated by the contraction of the muscles.

One of the largest of these rediae (Fig. 15) measures 1.36 mm. in length and 0.31 mm. in width, and the posterior limit of the voluminous intestine is 0.56 mm. from the anterior tip. The pharynx is very small in proportion to the size of the body, measuring 0.086 mm. in length and 0.065 mm. in width. The intestine contains dark brown materal evidently from the liver of the host. Bunched around the anterior tip of the redia just back of the oral sucker are elongate unicellular glands of the type often found in rediae, which send forward ducts to open near the tip.

The cuticula and muscle layers of the rediae of *Cercaria inhabilis* are quite thin. The circular muscles are the strongest but do not show externally. Inside of the muscles except in the region of the anterior part of the intestine and the germ gland, the wall is made up of a layer of cells which is thin in the older forms. In none of the rediae are embryos much differentiated, the largest showing mere stumps of tails, the beginning of suckers and traces of eye-spots. Since immature cercariae are found outside of the redia it is evident that they make their way out at a very early stage, and complete their development free in the snail's liver.

Since *Cercaria diastropha* resembles *Cercaria inhabilis* closely the description will be limited to pointing out the differences. As in *Cercaria inhabilis* different stages of development of the cercaria are found free in the snail. The mature cercariae extended and contracted their bodies very actively but none were noted swimming freely. This may have been due to the condition of the material studied. There was no check on the one examination.

Cercaria diastropha (Fig. 23) is cylindrical in cross section, pointed anteriorly, and when not contracted or flattened the region in front of the acetabulum is but little wider than that sucker. In living specimens the body varied from 0.27 to 0.54 mm. in length according to the state of contraction, and the width changed from 0.20 to 0.08 mm. The tail is always shorter than the body, being 0.22 mm. to 0.38 mm. in length and with an average width near its base of 0.054 mm., The tail is attached dorsad to the acetabulum, which is terminal and forms a flattened base for the conical body (Fig. 24). The oral sucker is elongate and in a specimen of average contraction has a length as great or greater than the acetabulum. In an animal about the state of contraction of Figure 23 the oral sucker had a length of 0.11 mm. and a width of 0.065 mm. and the acetabulum had a diameter of 0.105 mm.

The eye-spots are like those already described but are larger in proportion to the size of the body than in *Cercaria inhabilis*. Except for a very limited area around the eyes *Cercaria diastropa* is entirely unpigmented.

The body is filled with cystogenous glands from the oral sucker to the acetabulum.

On account of the freedom from pigmentation it was possible to work out the excretory system further in *Cercaria diastropha* than in *Cercaria inhabilis*. Figure 23, ex, shows the relations of this system. The tail vessel and the bladder are alike in both forms. The much convoluted crura of *Cercaria diastropha* which are large and contain scattered concretions, extend as unbranched vessels up to the region of the eyes. There they receive small branches from all parts of the body. It was possible to trace the largest of these branches altho on account of the cystogenous glands, the flame cells and the smallest ducts were not found. Into the tips of the crura open on each side two vessels, one from the side of the oral sucker and one from the posterior end. The posterior branch is soon divided into an outer and an inner vessel, which subdivide to reach all parts of the posterior body region.

The digestive system in *Cercaria diastropha* is similar to that of *Cercaria inhabilis,* but the oral sucker and its pouches are larger in proportion to the size of the acetabulum, and the intestinal ceca reach nearer the posterior end of the body.

In *Cercaria diastropha* the anlage of the reproductive organs is further developed than in *Cercaria inhabilis.* It is differentiated into four clearly separated areas, which bear the same general relation to the adult organs as in the other species. They are not however connected with strands of nuclei and are not in exactly the same relative position as in *Cercaria inhabilis.*

The above descriptions show that *Cercaria inhabilis* and *Cercaria diastropha* differ considerably in the size and shape of the body, the ratio in size of the suckers and in the position of the acetabulum, the amount of pigmentation, and in the anlage of the reproductive organs.

Rediae of *Cercaria diastropha* (Fig. 25) were in different stages of development. No rediae were found in which other rediae were developing and in none were the cercariae further dveloped than in the rediae of *Cercaria inhabilis.* The rediae were very mobile, having remarkable power of changing their shape, and with the aid of the posterior locomotor appendages could move fairly well. In the younger rediae the body would sometimes be extended to five or six times the length when contracted. This mobility is correlated with the extereme development of the circular muscles, which show clearly as annular bands (Fig. 25, ab). In the young living redia part of the excretory system could be made out. One longitudinal trunk from the anterior extremity was traced until it met two trunks from the posterior end.

In the youngest redia studied there were practically no germ balls in the body cavity; the length of a toto mount slightly contracted was 0.45 mm. and the greatest width 0.13 mm. The intestine extended to a point 0.22 mm. from the anterior end and was relatively voluminous. The oral sucker had a length of 0.43 mm. and a width of 0.032 mm. One of the largest specimens measured 0.78 mm. in length and 0.16 mm. in width. The intestine reached one-third the body length. The oral sucker was about the same size as in the younger specimens, the length being 0.044 mm. and the width 0.038 mm. From the above description it is evident that the redia of *Cercaria diastropha* is very much like that of *Cercaria inhabilis.* The greatest difference is in a greater mobility correlated with a greater development of the circular muscles in the former.

Altho a large number of adult trematodes belonging to the family Paramphistomidae has been described, I have found in the literature

mention of only three cercariae belonging to this group. The cercaria of *Diplodiscus subclavatus* has been known for a long time, having been first described by de Filippi and best described by Looss (1892:162-166). Of the two other forms one was first described by Sonsino (1892) as *Cercaria pigmentata,* and later shown experimentally by Looss (1896:-185-191) to be the larval form of *Amphistomum conicum (Paramphistomum cervi).* The other was also described by Looss (1896:177-185) as the larva of *Gastrodiscus aegyptiacus.* This conclusion, however, only rests on the structural comparison of the cercaria and the adult.

The five amphistome cercariae now known belong to two different sub-families of the *Paramphistomidae.* The cercaria of *Paraphistomum cervi* differs from the others in lacking the pockets of the oral sucker, and in having a connection between the longitudinal crura of the excretory system. It belongs to the sub-family *Paramphistominae.* The other four of these cercariae are much alike and belong to the sub-family *Diplodiscinae.* They all have the retrodorsal pockets of the oral sucker, and the muscular enlargement of the esophagus at the bifurcation of the intestinal ceca. *Cercaria diastropha* differs considerably from the other three in its small size, lack of pigmentation and in the proportionally large size of the oral sucker. The cercaria of *Diplodiscus subclavatus,* that of *Gastrodiscus aegyptiacus* and *Cercaria inhabilis* are very similar. The first of these differs from the other two in the large size of the pharynx of its redia and in the small size of the intestine. *Cercaria inhabilis* is larger than Looss' cercaria of *Gastrodiscus aegyptiacus.* My measurements show that the oral sucker of this species is twice as large as his, and the acetabulum is very much larger. There is nothing in *Cercaria inhabilis* to correspond to the papillae found by Looss around the mouth of his form, and the intestine of the redia is much larger in his species.

The only adult trematode which I have found in the literature from the United States which resembles these cercariae in structure is *Diplodiscus temporatus* Stafford. This form has the retrodorsal pharyngeal pockets found in the cercariae and also the muscular thickening of the esophagus. The arrangement of the reproductive organs is such that those of the adult might be derived from the anlage of either of the above cercariae. As far as conclusions from comparative structure are concerned either *Cercaria inhabilis* or *Cercaria diastropha* might be the larvae of *Diplodiscus temporatus.* Infection experiments alone can clear up this point. It is evident, that Cary (1909) is mistaken in the larval form which he assigns to *Diplodiscus temporatus.*

Cary (1909) described as belonging to the life-history of *Diplodiscus temporatus* Stafford sporocysts and rediae, both containing cercariae

from *Goniobasis virginica* obtained near Princeton, New Jersey. In 1911 Cary sent me some of the material which he had used in the preparation of this paper, including specimens of *Diplodiscus temporatus* from his experimental tadpoles. A study of this material and a careful analysis of Cary's account has convinced me that he has described in this paper, two different species of larval trematodes neither of which belong to *Diplodiscus temporatus*.

The snails of the species *Goniobasis virginica* which he collected from the Delaware and Raritan canal near Princeton in the fall of 1908, contained rediae in which cercariae were developing, but those collected from the same locality in the spring of the following year and those from the Delaware river near Trenton, contained sporocysts in which cercariae were developing. Cary assigns both these stages unhesitatingly to the same species, for no other reason so far as can be judged than that they were collected from the same species of snail from the same general locality. That in the same species of trematode, cercariae should be found developing from both sporocysts and rediae is without parallel. Further in his own descriptions Cary shows that he is dealing with two separate types of larvae. In connection with his account of the development of the cercariae in the sporocysts, (p. 643), he writes of the cercaria.

"In the dorsal part of the sucker (oral sucker) there is developed the dart (Stachel). This lies in a thin structureless sheath between the muscle cells. It is shaped like a short arrow with a comparatively broad head."

Neither in the description nor in the figure (Cary, 1909, Pl. 30, Fig. 6) of the cercaria which develops from a redia is a dart shown. Further a comparison of the cercariae developing from rediae with the others developing from sporocysts from the material which Cary sent me, shows that they are entirely different in practically every character. Figures 26 and 27 are drawings made to scale of these two types of cercariae. According to Lühe's (1909) classification of the cercariae these forms would fall into two entirely unrelated groups. The smaller one with the boring spine which develops in the sporocysts (Fig. 26) very evidently belongs in the Xiphidiocercariae (Lühe, 1909:189-200) while the larger form agrees with the characteristics of the Gymnocephalous cercariae (Lühe, 1909:182-186). That two such diverse cercariae should develop into the same adult is utterly impossible. Since in his infection experiments Cary uses only the cercariae which develops from rediae, he certainly can have no evidence that the cercariae which develops from sporocysts and are entirely different from the first type have any connection whatever with *Diplodiscus temporatus*.

Therefore Cary's whole discussion in the embrological part of the paper (pp. 617-647) which is based on the study of the sporocysts and the cercariae developing in them cannot without further evidence be given a place in the life-history of *Diplodiscus temporatus.* Since it proves the thesis that Cary sets out to make that the embryo in the sporocysts develops from parthenogentic eggs, this account is a very important contribution to trematode embrology.

Another point in Cary's paper which is very striking is the great difference between the cercaria which he describes as belonging to *Diplodiscus temporatus* and other amphistome cercariae, especially that of *Diplodiscus subclavatus,* of which Looss has worked out the life-history (Looss, 1892). A comparison of these two forms shows striking differences in the shape and size of the body, in the size and position of the acetabulum, in the excretory system especially that of the tail, and in their activities and encystment. (Compare Cary, 1909, Pl. 30, Fig. 6 and Looss, 1892, Pl. 20, Fig. 20). That cercariae belonging to the same genus should be so different in structure is contrary to all the accepted views of trematode development. The few observations found in the literature on the life-histories of closely related species of trematodes show a closer structural correspondence betweeen the cercariae than the adults.

A study of Cary's material shows that he is in error in the description and drawing of the largest of the two cercariae in certain fundamental points. In his drawing (plate 30, Fig. 6) and description the digestive system of the cercaria corresponds to that of the adult *Diplodiscus temporatus,* in having pharyngeal pouches and in the muscular enlargement of the esophagus at the point of division into the intestinal ceca. In his material the cercaria has no pharyngeal pouches and the clearly circumscribed pharynx which is followed by an enlarged portion of the esophagus is entirely different from his description and drawing for this form. Compare figure 27 and Plate 30, Figure 6 of Cary's paper. In fact, the digestive system of his so-called cercaria of *Diplodiscus temporatus* does not in reality correspond to that of the adult as his drawing and description suggest. Cary is also in error in his description of the tail of this cercaria, since the material which he sent me shows that it is much longer than he figures it and has a truncated end (Fig. 27). Neither does the reproductive anlage of this cercaria agree with his description and drawing (p. 606, Pl. 30, Fig. 6), for instead of three definitely circumscribed areas two in front of the acetabulum and one behind, it really consists of a small mass just in front of the excretory vesicle connected with a mass in front of the acetabulum by a line of nuclei.

When the adult *Diplodiscus temporatus* is compared with the larger of the cercariae which Cary assigns to it certain differences of structure are noted so fundamental that it seems impossible that the two forms can be the same species. Compare figures 27 and 28. The adult is a typical amphistome with the conical body terminating in a very large acetabulum, while the cercaria is widest toward the anterior end, flattened and its acetabulum which is only a little larger than the oral sucker is just back of the center of the body. Certainly very remarkable changes in shape and position of the organs would be necessary before the cercaria which developed in rediae in *Goniobasis virginica,* which Cary described, could metamorphose into an adult *Diplodiscus temporatus.* Cary makes no attempt to bridge this gap altho it would seem from his infection experiments that intermediate stages should have been obtained. It is especially hard to believe that the ventral sucker could have migrated from the middle of the body to the posterior end and have become so much larger in proportion to the oral sucker, and that the digestive system could have changed so fundamentaly as would have been necessary. In those species of trematodes in which the development is known the digestive and excretory systems are very much alike in the cercariae and in the adults. The principal changes come in the development of the reproductive organs and the corresponding enlargement of body regions, usually the post-acetabular.

The infection experiments that Cary conducted to prove the connection between this cercaria and *Diplodiscus temporatus* seem convincing until they are carefully analyzed. To carry conviction they should have been better controlled, described in more detail and the stages of development worked out. That I may do Cary no injustice I will quote in full his account of the experiments that he used to prove the connection between the cercaria and the adult (Cary, 1909: 612-1613).

"On Oct. 30 a number of tadpoles of *Rana catesbiana* were secured and several put in each jar containing infected snails. The tadpoles came from a pond in the grounds of the Biological Hall of the University of Pennsylvania, where *Goniobasis* is not found, so it seemed improbable that they would be infected with the parasite that was found about Princeton. As an added precaution all of the tissues of three of the tadpoles were carefully examined without finding parasites of any kind. When the tadpoles had been for a week in the jar containing the encysted cercariae, a dead individual was found. This one was examined for the presence of parasites with the following results: Nine worms, which from the condition of the sexual organs could be recognized as young, were found in the intestine of this tadpole. The other

organs of the body were entirely free from parasites. The worms in the intestine were about 2.5 mm. in length and 1 mm. in diameter at the posterior end. All of them were found in the last third of the intestine of the tadpole, scattered throut that part of its length. During the time that they were under examination, as was also true in every other instance, the worms remained attached to the intestine of the host by a large posterior sucker. The anterior part of the body was in almost constant motion.

"Others of the tadpoles used in the experiment died from time to time and were examined for the presence of worms. The result of the examination was identical in every case. A greater or less number of worms, ranging from ten to thirty-one, was found in the posterior part of the intestine. In no case were any of the worms, or any other recognizable parasites, found in any of the other organs of the tadpoles.

"The intestines of two of the tadpoles at the time of death contained worms still within the cyst. Among the others, individuals of different ages could be recognized so it was definitely established that the tadpoles could serve as the host for the sexually mature worms.

"Since it seemed probable from the number of worms found in each of the dead tadpoles that they had in many instances been the direct cause of the death of the host, some larger tadpoles were secured for further experiments. These were put into jars containing encysted cercariae; but after they had remained there for a few days they were transferred to a jar in which there had been no snails. A tadpole from this jar was killed each week to note the development of the parasites. The conditions of the environment proved unfavorable for the tadpoles and the last one of them died on Jan. 19, 1909, after having been infected with *Diplodiscus* nine weeks. The worms which were taken from the intestine of this tadpole had fully developed sexual organs, but, so far as could be determined from the condition of the jar, no eggs had been laid, or at least no embryos had been developed."

An analysis of these experiments shows a number of weaknesses. The fact that the tadpoles came from a pond in the grounds of the Biological Hall at the University of Pennsylvania offers no check on the results. The location of the pond at Philadelphia and not at Princeton and the fact that *Goniobasis* does not occur there, can hardly be called evidence that *Diplodiscus temperatus* is not present in great numbers. The only check that Cary gives on his experiments is the examination for parasites of three tadpoles out of the whole lot. These he reports free from all parasitic infection. This does not prove that the others were uninfected. The three examined may have been without parasites while the rest were infected, or it is even possible that the

parasites may have been overlooked. Any man even if somewhat accustomed to examinations for parasites is likely to overlook them, especially if they are small and the infection light, until a chance finding directs his attention to a particular organ. Therefore it would seem that the above experiments were not sufficiently controlled to prove that no infection of *Diplodiscus temporatus* was present in the tadpoles previous to the experimental feeding.

For infection he puts the tadpoles in the jars with infected snails and when a week later one of the tadpoles proved to be infected with nine immature specimens of *Diplodiscus temporatus* he concluded that they had developed from the larvae in the snails. A comparison of the structure of the two forms shows how improbable this is. The largest cercaria of this type in the alcholic material, which Cary sent me, had a body, 0.40 mm. in length and 0.20 mm. in width and an acetabulum 0.065 mm. in diameter. The only measurements that Cary gives in his description, which were evidently taken from a living specimen, are 2 mm. in length for both body and tail and 0.15 mm. in width. The tail is usually at least as long as the body, so that would make the body of the cercaria not over 0.1 mm. in length. Cary gives no measurements for the acetabulum but his drawing (Pl. 30, Fig. 6) shows it less than half the width of the body.

Since the cercariae must have had about the size, shape, and proportions given above at the time this tadpole was supposed to have eaten the cysts, their metamorphosis surely must have been extraordinary to have developed in a week into the immature specimens of *Diplodiscus temperatus,* which Cary found in the tadpoles. He describes these forms as 2.5 mm. in length, 1 mm. in diameter at the posterior end, and as being attached by the typical large posterior sucker. The posteror sucker of the young *Diplodiscus temporatus* (Fig. 28) has practically the width of the posterior end, which in this case would be almost 1 mm. Therefore if Cary's contention be correct his cercariae in one week almost tripled their length, changed the whole shape of the body, and increased their width five times. The acetabulum must in some way have jumped from the center of the body to the posterior extremity and increased its diameter ten times. Since such a transformation is impossible one is forced to conclude that the tadpoles used in the experiments were already infected with *Diplodiscus temporatus,* and that there is no connection between this species and the cercariae used in the experiment. The fact that according to Cary every tadpole examined was infected with *Diplodiscus temporatus* cannot be taken as attesting the success of the experiments but merely the general uniformity of the original infection. A detailed comparison of figures 27 and 28

shows how fundamental are the differences between the cercariae used in the experiments and *Diplodiscus temporatus.*

The second experiment is even less convincing than the first because no check whatever is given and the source of the tadpoles is not indicated, altho it is perhaps to be taken for granted that they are obtained from the same source as the first batch. These tadpoles were killed each week to note the development of the parasites and stages of *Diplodiscus temporatus* were found. If the development had followed the course that the writer maintains it would have been possible with this material to find transitional stages in change of shape, supposed migration of the acetabulum, etc. This Cary has not done and even the possibility seems to have escaped his notice, since it is not mentioned in the paper.

The following points have been proved in the above discussion.

1. That Cary described two entirely different species of cercariae as belonging to *Diplodiscus temporatus;*

 a. Those with stylets, which develop in sporocysts,

 b. Larger forms without stylets which develop in rediae.

2. That since the second type only were used in the infection experiments, no connection between the first type and *Diplodiscus temporatus* can have been shown.

3. That the infection experiments were not sufficiently controlled to be conclusive.

4. That the cercariae used could not have possibly developed into *Diplodiscus temporatus,* since the two forms differ so fundamentally in structure.

Since the stylet form of Cary's two species, which I have named *Cercaria caryi,* is very small, and no living material is available, it does not seem wise at the present time to attempt a detailed description. Figure 26 gives the most salient features. From the presence of the stylet, the small number of the stylet glands, and the small size of the acetabulum it may be placed with the Xiphidiocercariae in Lühe's group of the Cercariae microcotylae (Lühe, 1909: 196-198).

I was fortunate enough to obtain further material of the larger form, so that a detailed description of it is possible. On account of the great length to which the tail is sometimes stretched I shall describe it as *Cercaria megalura.*

DISTOME CERCARIAE

The great bulk of known cercariae belong to this division. In my material are eleven distome cercariae representing eleven of the principal sub-groups.

GYMNOCEPHALOUS CERCARIAE

Since beyond the fact that they develop in rediae the cercariae placed in this subdivision agree only in the absence of certain characters, it is without doubt an unnatural group. However in the present state of our knowledge it is convenient to retain it. Of my material only *Cercaria megalura* belongs here. This species and its allies differ so much from all the other cercariae of the gymnocephalous group, that I propose to make them the basis of a new sub-group, to which the name Megalurous or heavy-tailed cercariae may be given.

MEGALUROUS CERCARIAE

From 73 specimens of *Pleurocera elevatum* from the Sangamon river near Mahomet, Illnois, examined during November and December, 1913, one was found with the liver packed with rediae in which developed a very peculiar kind of cercaria. Comparison showed this form to be the same as the larger cercaria which Cary assigns to *Diplodiscus temporatus*. Since Cary's account is not very complete, obscured by a mistaken viewpoint, and incorrect in many particulars, a further description of this species seems advisable. Altho many of the cercariae seemed fully matured, none were found free in the organs of the snail and no rediae were found which contained rediae.

Living rediae and cercariae of *Cercaria megalura* moved actively. The redia was very active and the region back of the posterior locomotor appendages on account of its mobility and attenuation resembled a tail. The anterior portion of the body also could be extended and contracted freely and with the aid of the locomotor appendages locomotion was possible. The cercaria was unable to use its tail for swimming in open water but on a substratum it moved fairly rapidly with the aid of the suckers. With the acetabulum attached the anterior end would reach out and the oral sucker take hold. The acetabulum would then loosen

its grip, and the body contract until the suckers were close together. The acetabulum would again take hold just back of the oral sucker, which would in its turn become loosened and extended. Locomotion consisted in a continued repetition of these movements. During this process the tail was contracted and took no part in the movement. At certain times a cercaria became attached by the posterior tip of the tail, which is furnished with an adhesive organ. The animal then extended to five or six times its usual length, and became greatly attenuated. While in this position the cercaria moved continually with a wriggling motion. Looss (1896:202) noted a similar activity in *Cercaria distomatosa* Sonsino from *Cleopatra bulimoides* Bourg., from Cairo, Egypt, a form very much like *Cercaria megalura.* This cercaria became attached by the extremity of the tail to the surface of the water or to some bodies such as plants or branches of trees very near the surface of the water, and moved in a serpentine manner like a tubificid worm. This comparison would apply equally well to *Cercaria megalura.* What relation this peculiar habit has to the future development of the cercaria is not known.

No cercariae were found encysting altho large numbers had extruded cystogenous material in the form of a sort of open tube around the body (Fig. 30). In fact this seemed to be the normal procedure when the animal came in contact with fresh water. Cary (1909:609-610) performed experiments with some of his specimens of *Cercaria megalura* which showed that this extrusion of cystogenous material was due to the change from the conditions in the liver of the snail to fresh water. Looss (1896:201-203) found no free individuals of *Cercaria distomatosa* in which the cystogenous material was still in the glands, and he also mentioned that when the cercariae were taken up in a pipette they became encysted as quick as a flash. He noted further that they encysted also in the open, loosening their hold and dropping to the bottom after having lived for a period free.

The redia (Figs. 31 and 36) of *Cercaria megalura* is an elongate sac slightly tapering toward the anterior end, with the posterior locomotor appendages about six-sevenths of the distance from the anterior to the posterior extremity. It is widest just in front of the appendages and tapers almost to a sharp point posteriorly. The birth pore is on the dorsal side just back of the pharynx.

The mouth of the redia is at the anterior tip and the oral cavity opens into a short, narrow passage, which widens out almost immediately into the voluminous digestive tract. This extends back of the posterior locomotor appendages nearly to the end of the body. In cross sections (Fig. 35) the intestine occupies from one-third to two-thirds of the body

cavity depending on the amount of food material present and the pressure from the developing cercariae. In the inner lining of the intestine were found flattened, scattered nuclei, but no cell boundaries could be distinguished. The body cavity occupies most of the entire region from just back of the oral sucker up to the posterior tip, but does not extend into the posterior locomotor appendages and the tail-like posterior extremity. These regions are filled with parenchymatous tissue in which definite cell boundaries could be determined (Fig. 35). The wall of the body cavity of even the youngest redia is very thin, and in the inner lining of flattened pavement cells with flattened nuclei, the cell boundaries could be distinguished only with difficulty. A small germ gland consisting of but few differentiated cells is present at the posterior extremity of the body cavity.

All ages of rediae were present in the snail from those in which the oldest contained cercaria was scarcely differentiated at all, to those in the body cavities of which there were from four to eight almost fully matured cercariae. The youngest redia studied (Fig. 36) which contained no cercariae having the cystogenous glands at all developed, was 0.53 mm. in length and 0.12 mm. in greatest width. The posterior locomotor appendages were 0.097 mm. from the posterior end, and the intestine extended to within 0.076 mm. of the posterior extremity. The pharynx was slightly elongated, being 0.049 mm. in length and 0.043 mm. in width. The body cavity contained a number of developing embryos only one of which was far enough along to be recognized as a cercaria. In this embryo (Fig. 36, cv) the tail was a mere stub hardly marked off from the body. The length of the body was 0.33 mm. and its width 0.054 mm., while the tail had a length of 0.038 mm. and a width of 0.032 mm. The sucker, digestive system, and reproductive anlage could be made out.

From one of the largest rediae studied the following measurements were taken (Fig. 31). The length was 1.16 mm., and the width 0.19 mm. The posterior locomotor appendages were 0.27 mm. from the posterior extremity, and the intestine, which filled about half the body cavity, extended to within 0.086 mm. of the posterior tip. There were four fully matured cercariae, one of which while still in the redia had extruded its cystogenous material, and a number of developing embryos of all ages. The pharynx of this redia was 0.054 mm. in length, and 0.049 mm. in width, showing almost no development in size from the very youngest redia.

The length and width of the body of *Cercaria megalura* (Figs. 29 and 30) vary greatly with the state of contraction. The tail varies from one-half the length of the body when the animal is moving on a

substratum to ten times that length when the cercaria is attached. The body is also about four or five times as long when extended as when contracted. At average extension the body is slightly pointed anteriorly and the acetabulum is but little more than half the distance from the anterior to the posterior end. The preacetabular region is a little wider than the postacetabular, and the postacetabular tapers slightly toward its truncated posterior extremity.

In mounted specimens the average length of the body is 0.4 mm., and the widest diameter of the preacetabular region averages 0.13 mm., while that of the postacetabular is 0.09 mm. The width of the tail at its base varies from 0.03 mm. to 0.054 mm., depending on the state of contraction. The oral sucker is lightly elongate, having an average length of 0.05 mm. and a width of 0.045 mm. The acetabulum is slightly larger and circular, averaging 0.054 mm. in diameter.

The structure of the tail of *Cercaria megalura* (Figs. 30 and 32) is interesting on account of its remarkable power of extension and the modification of its posterior end for attachment. It is truncated and there is an invagination at its tip. Into this inpushing open a clump of from 15 to 20 unicellular club-shaped glands. These glands have an average length of 0.017 mm. and width of 0.009 mm., and contain nuclei measuring 0.005 mm. in diameter. It is probable that these glands secrete some substance which makes possible the adhesion of the end of the tail. The tail is strongly attached at its base and except near the tip appears to be filled with vesicles, which are stretched out when the tail is extended and compressed when it is contracted. Figure 32 represents a cross section of the tail. The cuticula is very thin, the muscle layers reduced, and the great bulk of the tissue is made up of parenchymatous cells, the nuclei of which are surrounded by small masses of protoplasm. These cells are connected by strands of protoplasm and the large intercellular spaces which are filled with clear fluid give the appearance of vesicles. It is the looseness of the tissue of the tail which makes possible its remarkable changes in shape.

The cystogenous glands of *Cercaria megalura* are very highly developed and when the cystogenous material is still present in them they from the bulk of the whole body. These glands (Fig. 33 cs) are large, elongate, club-shaped cells, most of which open on the ventral surface, a few only opening dorsally. They are full of tiny, rod-shaped, cystogenous granules. The cells have an average length of 0.036 mm. and a width of 0.012 mm., and contain at about their centers large nuclei. They are present all thru the body of the cercaria from the posterior limit of the oral sucker almost to the posterior extremity. A comparison of cross sections of two cercariae at the region of the esophagus shows

the striking changes made in the glands and all the tissues by the extrusion of the cystogenous material (Figs. 33 and 34). The cystogenous glands in figure 34 have become much reduced in size, their cytoplasm is only slightly granular, and even their nuclei appear to have shrunk. In fact they are distinguished only with difficulty from the body parenchyma. The extruded material forms a layer about 0.0075 mm. in thickness, closely adhering to the animal. After the extrusion of the cystogenous material the cercaria becomes somewhat shorter, broader, and thinner than before.

The mouth of *Cercaria megalura* is subterminal and the oral cavity leads into a narrow prepharynx about the length of the oral sucker but varying greatly with the state of contraction. The pharynx is small, measuring on the average 0.022 mm. in length and 0.020 mm. in width, and opens by a narrow passage into a much wider portion of the esophagus. This soon divides into the narrow intestinal ceca which reach almost to the posterior end of the body. The lining of the enlarged portion of the esophagus and the intestinal ceca is formed by flattened pavement cells with flattened nuclei, which are illustrated in figures 33 and 34. Figures 29 and 30 both show the relations of the digestive system.

At the posterior end of the body is found the pyriform excretory vesicle which also has its walls formed of flattened cells with flattened nuclei. From the anterior end of the vesicle pass forward two longitudinal vessels which can be followed to the region of the pharynx (Fig. 30). The excretory pore was not distinguished. In *Cercaria distomatosa* Looss (1896:200) described the excretory system as having a short common trunk in the tail, leading from the bladder and opening to the outside by two short ducts. Cary in his material of *Cercaria megalura* located the excretory pore as dorsal just at the base of the tail, and found no extension of the excretory system into the tail. The most careful examination of the anterior part of the tail of *Cercaria megalura* in living specimens, toto mounts, and sections showed no trace of excretory tubules.

The anlage of the reproductive organs (Fig. 30 ra) appears as a small mass of nuclei just in front of the excretory bladder; from this a line of nuclei extends forward to join another small nuclear aggregation just in front of the acetabulum. No definite outlines of organs could be determined. The mass just anterior to the acetabulum represents to the ends of the reproductive ducts.

In the literature are found descriptions of only two cercariae resembling *Cercaria megalura: Cercaria distomatosa* Sonsino best described by Looss (1896:197-204), and a cercaria from the Hawaiian

Islands from *Melania baldwini* Annecy and *Melania newcombii* Lea, described briefly by Lutz (1893:327). Since in these forms there are no fixed larval organs such as spines, stylets, etc., to compare, specific differentiation is difficult. *Cercaria distomatosa,* however, seems to show some constant differences from *Cercaria megalura.* In *Cercaria distomatosa* the rediae reached a length of 1.8 mm., had a pharynx 0.07 mm. long, and a digestive system extending only to the posterior locomotor appendages, which are about three-fourths of the distance from the anterior to the posterior end. Also rediae were found in which rediae were developing. In *Cercaria megalura* as noted above the digestive system was more voluminous and reached almost to the posterior end of the body, and the posterior locomotor appendages were further back, being about six-sevenths of the distance from the anterior to the posterior end. Also Looss' measurements for *Cercaria distomatosa* are slightly larger than those for *Cercaria megalura,* and the judge from his figure and description, the tail is considerably smaller. He found the final tubules of the excretory system in the tail, which were not found in my species. The Hawaiian cercaria described by Lutz (1893:337) seemed to be similar to *Cercaria megalura* and *Cercaria distomatosa* in having a long tail by which it can become attached, in the general relationship of the body structures, and in the form of the cyst. A more detailed comparison is impossible on account of the meagerness of Lutz's description.

It is evident that these three forms are very closely related. Cary's attempt to relate *Cercaria megalura* to *Diplodiscus temporatus* is the only suggestion as to the life-history of a member of this group, but as shown above, this cannot be accepted.

ECHINOSTOME CERCARIAE

Cercariae belonging to the family *Echinostomidae* are very easily recognizable on account of their structural correspondence to the adults. It is impossible to subdivide them into smaller natural groups. The following may be given as a brief statement of characters for the Echinostome cercariae.

1. Distome cercariae developed in rediae.
2. Rediae have collar, birth-pore, and posterior locomotor appendages.
3. Cercaria with digestive system consisting of prepharynx, pharynx, long esophagus, and intestinal ceca reaching the posterior end of the body.
4. Anterior end of cercaria with collar and circle of spines.

5. Excretory system opening on each side of the anterior part of the tail; excretory bladder small, crura large, reaching to oral sucker.

6. Tail powerful, longer than body.

In the material used in this study were two echinostome cercariae.

The first species was found in several specimens of *Planorbis trivolvis,* examined during November, 1913, from a small pond near Urbana, Illinois. The infection consisted of rediae containing cercariae in the livers, and encysted cercariae in the body cavities of the snails. *Planorbis trivolvis* is then able to serve both as intermediate and secondary intermediate host for this species. I propose for this cercaria the name *Cercaria trivolvis.* The second of these larvae was found in a few out of thirty-six specimens of *Campeloma subsolidum* from Hartford, Connecticut. The snails in this case I regard simply as the secondary intermediate host since no rediae were found. From the fact that the encysted cercaria had a pinkish tinge produced by pigment granules in the postacetabular region the name *Cercaria rubra* is proposed for this species.

Cercaria trivolvis (Fig. 39) completes its development before leaving the redia. Therefore very few cercariae were found free in the liver of the host. That a certain time is spent in free life is suggested by the fact that altho free swimming cercariae were kept under observation for a whole day none were seen to encyst. There seemed to be no connection between infection in the liver and cysts in the body cavity, since altho a few snails had both types of infection the majority had only one.

This cercaria (Fig. 39) moved actively both in open water and on a substratum. The tail was powerful and extended when the animal was swimming to two or three times the body length. For the swimming movement the cercaria bent ventrad almost double, with the posterior half of the body almost directly dorsad of the anterior. The tail which extended beyond the anterior end lashed vigorously and propelled the animal rapidly. When a cercaria came in contact with a surface it took hold with its suckers and moved actively with a creeping movement similar to that already described for *Cercaria megalura.* The structure and position of the crown of spines suggests that it would be of considerable aid to the animal in making its way thru connective tissue.

The cysts of this species were oval, having an average length of 0.16 mm. and width of 0.15 mm. The cyst wall varied in thickness from 0.007 mm. to 0.012 mm.

Cercaria trivolvis (Fig. 39) is elongate, pointed anteriorly, and has its greatest width in the region of the acetabulum. It has an heart-

shaped anterior end with a crown of thirty-seven spines. Well extended toto mounts have an average length of 0.38 mm. and a width of 0.12 mm. The tail is large and powerful in proportion to the size of the body, and in a state of average extension has a length of 0.50 mm. When contracted it may have a length considerably less than that of the body and when the cercaria is swimming it often reaches to two or three times that length. It ends in a sharp point and at the tip for about 0.05 mm. to 0.06 mm. it is narrow and is composed only of the muscle layers, lacking the parenchymatous core.

The oral sucker is almost exactly spherical and has an average diameter of 0.043 mm. The acetabulum is a little larger, being 0.049 mm. in diameter, and is situated two-thirds of the distance from the anterior to the posterior end.

The body from the anterior end to the acetabulum is set thickly with rows of small spines, only visible under the highest powers of the microscope.

The crown contains thirty-seven spines of equal size, arranged in two alternate rows, broken in the middle of the ventral surface. They are arranged regularly except for the two or three nearest the mid-line on the ventral side, which point in.

The body from the oral sucker to the attachment of the tail is filled with cystogenous glands. They are unicellular and club-shaped and all open on the dorsal surface.

The oral sucker is followed by a typical prepharynx about 0.022 mm. in length. The pharynx is round, on the average 0.017 mm. in diameter. The esophagus and intestinal ceca are not yet functional, but appear merely as columns of granules enclosed in membranes and containing irregular spaces representing the beginning of the lumina. The esophagus is long, reaching almost to the acetabulum, and the ceca reach nearly to the posterior end of the body.

Cercaria trivolvis (Fig. 39) has the typical echinostome excretory system. The portion in the tail was made out with great difficulty and is apparently not functional. A vessel passes back from the excretory bladder for one-fifth or one-sixth of the length of the tail and sends out two lateral branches which open to the outside. Dorsally at the base of the tail is the adult excretory pore which apparently at this stage gives passage to the outside for the waste material, since altho the vesicle kept filling and emptying the vessels of the tail did not change their caliber. In the oldest specimens the crura are large and distended from the bladder to the region of the pharynx with regularly-shaped, highly refractive granules. For the most part these are round or oval, but some of them appear to be compounded of from two to four of the

round ones. At the region of the pharynx the excretory tubules are much smaller and curve around forming a characteristic loop, from which a small vessel on each side could be traced back to the level of the acetabulum.

The nuclei which form the anlage of the reproductive organs of *Cercaria trivolvis* are not yet fully divided into separate masses. In the midline of the body just in front of the excretory bladder and behind the acetabulum is an elongate mass of these nuclei from which a line can be traced forward to a smaller mass in front of the acetabulum. The posterior mass probably develops into the ovary and testes, and the anterior mass represents the ends of the reproductive ducts.

Rediae of *Cercaria trivolvis* (Figs. 37 and 38) were present in the infected snails in various stages of development. The youngest were unpigmented but in the older ones orange colored pigment had developed in the outer wall, which rendered the largest rediae almost opaque.

The smallest redia found had a length of 0.30 mm. and a width of 0.065 mm. The posterior locomotor appendages were 0.22 mm. from the anterior end and the region back of them was attenuated and pointed. The oral sucker had a length of 0.041 mm. and width of 0.043 mm. and the intestine, which was very narrow and elongate, reached to the posterior locomotor appendages. No germ balls were present in the body cavity which was but little larger than the intestine, and the region of the germ gland was not visibly differentiated.

In a redia (Fig. 38) 0.41 mm. in length and 0.081 mm. in width the posterior locomotor appendages were 0.34 mm. from the anterior end. A ridge extended around the body like a welt 0.086 mm. from the anterior end. The body cavity at this stage had become well developed and contained germ balls, none of which however were in front of the posterior extremity of the intestine. The pharynx had a length of 0.043 mm. and a width of 0.046 mm. and the intestine, which was wider than the earlier stage and contained dark material, reached more than one-half the body length.

The great majority of rediae found were well advanced in development and contained mature cercariae in their body cavities (Fig. 37). The body cavity had increased in size extending from the birth-pore almost to the posterior end, and into the posterior locomotor appendages. In each redia were germ balls and from two to four mature cercariae, the bodies of which were from one-third to one-half the total length of the redia. In a mature redia 0.81 mm. in length and 0.15 mm. in width, the posterior locomotor appendages were 0.62 mm. from the anterior end. The pharynx was 0.041 mm. long and 0.043 mm. wide and the intestine which was somewhat distended with food material and

pushed ventrad by the cercariae, extended for more than one-third of the length of the body.

The pharynx is about the same size in the youngest and the oldest rediae, and the actual size of the intestine differs but little, altho its ratio to the size of the body is much less in the older form. The birth-pore is located on the dorsal side of the body a little back of the pharynx. In the oldest rediae the anterior collar is not present and the posterior locomotor appendages are much reduced.

Cysts of *Cercaria rubra* (Fig. 41) were present in the tissue above the gills of six of the thirty-six specimens of *Campeloma subsolidum* from Hartford, Connecticut. The cysts were large, round, thick-walled, and of very uniform size, measuring 0.195 mm. to 0.205 mm. in diameter. The cyst wall was transparent and had a thickness of 0.016 mm. The worm almost completely filled the cyst with practically the whole dorsal surface against the wall, and the posterior end overlapping the anterior.

Several cysts were opened and the worms freed. A study was made of these while living but none were preserved.

The living cercariae (Fig. 40) were on the average 0.50 mm. in length and 0.15 mm. in width at the region of the heart-shaped anterior end. They tapered slightly posteriorly, had a width at the acetabulum of 0.13 mm. and the end was bluntly rounded.

The oral sucker of *Cercaria rubra* was a most exactly round having a transverse diameter of 0.043 mm. and the acetabulum which is two-thirds of the distance from the anterior to the posterior end was larger, measuring 0.065 mm.

The collar which is typical of the Echinostomes is very well defined in this species and has arranged around its edge in two alternating rows, forty-three spines, which vary only from 0.018 mm. to 0.022 mm. in length. In the middle of the ventral surface as is usual there is a depression and a break in the rows of spines. The four median spines on each side of this space are not in regular line with the others and point inward. Besides these eight there are seventeen spines in the upper row and eighteen in the lower row (Figs. 40 and 42). The surface of the body as far back as the acetabulum was covered thickly with rows of spines pointing backward. They were 0.005 to 0.007 mm. in length. The rows were 0.008 mm. apart and the spines were set thickly in the rows.

The digestive system (Fig. 40) offered nothing peculiar. The prepharynx had a length about equal to the diameter of the oral sucker, and the pharynx had a diameter of 0.025 mm. The short esophagus and

intesinal ceca contained the granules and their regular spaces described for *Cercaria trivolvis.*

Only the main branches of the excretory system could be traced. The crura were packed very full of concretions and the bladder was narrow.

Since this species was only studied alive the anlage of the reproductive system could not be distinguished.

In comparison with the large numbers of adult Echinostomes known the descriptions of but few larval forms are to be found in the literature. *Cercaria rubra* differs markedly from all of these in the number and arrangement of the oral spines. *Cercaria trivolvis* on the other hand agrees very closely with *Cercaria echinata* von Siebold. This form is not sufficiently described to make a detailed comparison possible. Lühe (1909:188) gives to it thirty-seven spines of equal size in the crown, altho the earlier writers counted only thirty-six. The intestine of the redia is shorter in *Cercaria echinata* than in *Cercaria trivolvis,* and the size of the oral sucker in comparison to the acetabulum is less in the former than in the latter species.

A number of suggestions have been made in regard to the adults corresponding to the European species of echinostome cercariae. None of these proposed relationships have been proved by experiments. Lühe (1909:65) recently made the following statement in regard to this group:

"von den bisher mit Namen unterschiedenen Cercarien (sämtlich aus Süsswasserschnecken) ist noch keine mit volliger Sicherheit auf eine bestimmte Art zu beziehen."

In England two echinostome cercariae have been assigned to adults on the basis of morphological comparisons. The cercariae were not given special names; the adults are *Echinostomum leptosomum* Creplin by Lebour (1907:447-451) and *Echinostomum secundum* Nicoll by Nicoll (1906:517-518).

None of the adult echinostomes from North America agree in the number and arrangement of the anterior spines with the two cercariae described above.

The following form, for which I propose the name *Cercaria reflexae,* and which was found in, some of the specimens of Lymnaea reflexo from Chicago, Ill., will be treated as an appendix to the Echinostome cercariae. The livers of the snails infected with *Cercaria reflexae* were packed with rediae in various stages of development of which the greatest numbers were large and full of numerous mature cercariae. Sections of the liver showed that but very few cercariae were free in its tissues but large

numbers were freed when the organ was removed from the snail. Also in the body cavities of numbers of the same snails were found encysted cercariae of the same species. That the cercariae were continually making their way out and encysting in new snails was shown by the fact, that while during the first few days after the snails came into the laboratory only a few contained the encysted cercariae, later all were infected.

The movement of *Cercaria reflexae* both in open water and in a substratum was exactly like that of *Cercaria trivolvis.*

The body varied greatly in size and shape. When contracted for locomotion it was nearly as wide as long. A fairly well extended mounted specimen (Fig. 43) is pointed anteriorly, widest at about the level of the acetabulum and narrower at the posterior end. The anterior end does not suggest the echinostome collar, and there is no crown of spines. One well extended specimen had a length of 0.46 mm. and a width at the acetabulum of 0.135 mm., with a thickness of a little more than half the width.

The tail at average extension has a length a little greater than the body, and an average width at its base of 0.05 mm. to 0.06 mm. The tail is provided with a dorsal and a ventral fin-like ridge which is narrow at its base and at its widest part equals about one-half the diameter of the tail.

The oral sucker has a diameter of 0.046 mm. and the acetabulum which is just back of the middle of the body is 0.06 mm. in width.

The surface of the body back to the region about half way from the acetabulum to the posterior end is covered with small spines arranged in rows and set closely together.

The whole body from the oral sucker to the posterior extremity contains large unicellular cystogenous glands which open dorsally, and fill the bulk of the body toward the dorsal side. These are like the cystogenous glands already described for *Cercaria megalura* and the amphistomes.

The oral cavity is followed by a short prepharynx and a small pharynx, 0.022 mm. in diameter. The esophagus and the intestinal ceca were very small and could only be followed in sections. The esophagus reaches almost to the acetabulum and the intestinal ceca to the posterior end.

The excretory system of *Cercaria reflexae* (Fig. 43, ex) is very much like that of *Cercaria trivolvis.* In the former species the vessels from the bladder to the tail are larger and serve to carry away the excretory products, for when the excretory bladder became contracted they became distended but soon again became reduced. The excretory crura too are smaller than in the other species. Opening into the

crura could be traced smaller vessels leading from the posterior end of the body, and forming a loop at the region of the pharynx similar to that of the echinostomes.

The nervous system shows very prominently both in living and preserved specimens and its larger branches can easily be traced. It shows nothing peculiar. From the large masses on each side of the prepharynx two branches pass out to the oral sucker. Laterally there are two branches on each side in the pharyngeal region, and strands can be traced almost to the posterior end of the body.

That the specimens of *Cercaria reflexae* which came under my observation were well along in development is attested by the condition of the reproductive anlage (Fig. 43). It is divided into four definite areas. In the region of the mid-line just in front of the excretory bladder are three masses of nuclei, one in front of the other and close together. The posterior two which are smaller than the other probably represent the anlage of the testes, while the anterior larger mass of nuclei the anlage of the ovary and the structures surrounding it. Just in front of the acetabulum is a mass of nuclei representing the future ends of the reproductive ducts. The course of the ducts connecting these areas could not be traced.

The rediae of *Cercaria reflexae* (Fig. 45) were present in different stages of development in the infected snails, altho there was a great preponderance of the fully matured forms. The smaller rediae were very active in extending and contracting their bodies, and were able to make progress with the aid of their posterior locomotor appendages. The largest forms were sluggish and reduced to mere sacs containing cercariae.

The smallest rediae have much the same structure as those of *Cercaria trivolvis*. One of them measured 0.28 mm. in length and 0.054 mm. in width and had the posterior locomotor appendages 0.22 mm. from the anterior end. The anterior ridge or collar was very prominent, 0.022 mm. from the anterior end, and the pharynx had a diameter of 0.043 mm. A number of small germ balls were present in the body cavity and the intestine extended to the region of the posterior locomotor appendages.

A redia somewhat larger than the one just described is shown in figure 44. In this form the cercariae are beginning to be developed into recognizable form.

The nervous system was quite well developed in the young rediae of this species. In one very immature specimen studied while alive two large nervous masses (Fig. 46, n) could be distinguished on each side of the posterior part of the oral sucker, which sent two branches

forward and two backward soon to become lost in the body wall. Very few observations on the nervous system of the redia are found in the literature. Looss (1896:199) traced the nervous system of the redia of *Cercaria distomatosa* about as far as it is followed in the above description. He speaks of this as the best developed of the nervous systems described in the redia up to that time. The degree of development of the nervous system as he suggests is correlated with the degree of mobility of the redia.

In the largest of the rediae (Fig. 45) almost all the germ balls have developed into mature cercariae, of which from twenty to thirty are present. The body cavity is much enlarged, the cercariae having pushed clear into the posterior tip, into the posterior locomotor appendages and up around the oral sucker. The rediae are mere shells, the anterior collar having been obliterated and the posterior locomotor appendages much reduced. The length of one of the largest rediae found was 2.26 mm., the width 0.30 mm. and the posterior locomotor appendages were 1.65 mm. from the anterior end. The oral sucker is very little different in size from that in the younger specimens, its diameter being 0.056 mm. The intestine was long and slender and reached to a point 1.15 mm. from the anterior end.

That *Cercaria reflexae* is closely related to the echinostomes is shown by a comparison with *Cercaria trivolvis*. The rediae of the two species have much the same general structure. In fact it would be practically impossible to distinguish between very young rediae of the two forms. Further, the locomotion and general body structures of the two cercariae are similar. The arrangement of the anlage of the reproductive organs of the two forms is much alike. That *Cercaria reflexae* is simply an immature echinostome cercaria in which the crown of spines has not developed is improbable from the fact that its other structures are those of a well advanced cercaria, the anlagen of the reproductive organs especially being considerably differentiated. No record has been found of any species either cercaria or adult which agrees with *Cercaria reflexae*.

MICROCERCOUS CERCARIAE

Among thirty-six specimens of *Campeloma subsolidum* from Hartford, Connecticut, four were found to be infected with rediae and very short tailed cercariae. The infection was in the tissues of the body above and at the bases of the gills. This form, which has a very short triangular tail, I propose to name *Cercaria trigonura*.

The cercariae were free in the tissues of the snail, were numerous, and were all in the same stage of development. When freed, they ex-

tended and contracted their bodies rapidly, the preacetabular region being the most active, but they were unable to swim. The tail, bent ventrad and pushing against the substratum, aided somewhat in locomotion, and at times the oral sucker was used for attachment. By this peculiar method the animal was able to make a little progress with a great deal of effort. Leuckart (1886:86) notes the same type of movement for *Cercaria limacis* Moulinié, a stumpy tailed cercaria from *Limax cineria.*

"Ausser Stande zu schwimmen, benutzen diese Wurmer den fast hertzformigen Schwanzanhang beim Kriechen als Nachschieber."
Some of these cercariae were kept alive and active in tap-water for three or four days.

Cercaria trigonura (Figs. 48, 50) has an elongate, cylindrical body, averaging in mounted specimens 0.24 mm. in length and 0.06 mm. in width. The oral sucker measures on the average 0.049 mm. in length and 0.039 mm. in width and the acetabulum which is slightly back of the center of the body is smaller, being 0.04 mm. in diameter. The cuticula is thin and at the anterior end beset with tiny spines, which are numerous over the oral sucker, thin out posteriad and disappear entirely back of the pharynx.

The tail of *Cercaria trigonura* is short, easily detached, grooved ventrally, and has the extremity bluntly pointed (Figs. 48, 50). It has an average length of 0.052 mm. and a width of 0.024 mm. Under the cuticula is a thin layer of circular muscles which are supplemented ventrally by a number of stronger longitudinal fibers that extend from the base to the tip. The size of these strands and the fact that they have no opposing muscles on the dorsal side would account for the fact that the tail is usually bent ventrad. The bulk of the tail is formed of loose parenchymatous tissue consisting of scattered nuclei, connecting protoplasmic strands and good sized vesicles.

On the ventral surface of *Cercaria trigonura* just at the base of the tail is a slit-like opening, which extends forward a short distance and dorsad reaches up into the body. Opening into this cavity are large numbers of unicellular glands which stain very heavily with haematoxylin. Figure 48 pg shows the relation of this posterior glandular structure. It is interesting that the shape and position of the tail give it the appearance of a short trough ready to carry off the secretions of this gland. The position and structure of the posterior gland suggest that it may function for adhesion. No activity which suggests such a function has been observed and for none of the other stumpy tailed cercariae has the description of a posterior glandular structure been found.

Set in the dorsal part of the oral sucker and protruding for about one-fifth of its length is a cephalic spine or stylet (Figs. 47, 49). The spine has a length of 0.018 mm. and a width of 0.004 mm., is sharply pointed and slightly thickened about two-thirds of the distance from the base to the tip. Ventrally no thickening is present.

The cephalic or stylet glands (Fig. 48, sg) fill the space dorsad and anteriad to the acetabulum and extend forward to just back of the nervous system. The individual glands are small, averaging 0.024 mm. in length and 0.012 mm. in width, finely granular and contain small nuclei. Their ducts pass forward dorsally over the oral sucker and open around the cephalic spine in the anterior pit. The numbers were so large that no accurate count could be made. They form a single mass unbroken in the median line.

The mouth is subterminal and back of the oral sucker is a small pharynx, 0.012 mm. in length by 0.01 mm. in width. The prepharynx is short and the esophagus and intestinal ceca are entirely undeveloped.

The excretory pore of *Cercaria trigonura* opens dorsally at the posterior extremity of the body just at the base of the tail. Leading up to it is a narrow tube near the dorsal surface which expands into the large bicornuate excretory vesicle, the horns of which reach on each side of the acetabulum. Vessels could be traced along the sides of the body from the tips of the horns of the vesicle up to the pharynx. Figures 48 and 50 give the relations of the pore vesicle and vessels. The vesicle is lined with a thick layer of granular, cuboidal, epithelial cells with large nuclei (Fig. 54, ex). An excretory vesicle with thickened walls of the character just described has been found in the other so-called stumpy-tailed forms.

The anlage of the reproductive organs shows as a mass of nuclei dorsal to the posterior part of the acetabulum (Fig. 48, ra).

Along with the cercariae in the tissues of *Campeloma subsolidum* were large numbers of rediae of different sizes. They were found in every snail infected with *Cercaria trigonura* and were not found in any instance where this species was not present. The only rediae that showed any activity were very small immature forms which were present in considerable numbers and in the same stage of development. They were active, extending and contracting and twisting and turning in all directions. Part of them were sharply pointed and the others bluntly rounded posteriorly. The first type (Fig. 51) was the most common and the structure of these will be described in some detail. The average of the mounted specimens of the small rediae is 0.019 mm. in length and 0.04 mm. in width. The pharynx is small, 0.03 mm. in width

and set back slightly from the anterior end so that the anterior part of the oral cavity is in front of it. The intestine is narrow and elongate reaching nearly to the end of the body and almost filling the small body cavity. Inside of the cuticula and muscle layers the wall is made up of embryonic nuclei with poorly defined cell boundaries. There are present no developing embryos and the germ gland is not clearly differentiated.

Very few rediae were found showing intermediate stages between the small type just described and the largest forms. The one shown in Figure 53 with only five germ balls of any size in its body cavity is 0.43 mm. in length and 0.09 mm. in diameter. The pharynx has the same width as length, 0.043 mm., and the pouch shaped intestine, which is 0.11 mm. long and 0.038 mm. at its greatest width, extends to a point only about one-third of the distance from the anterior to the posterior end. The body cavity is large and contains oval germ balls, the largest of which is 0.076 mm. long and 0.06 mm. wide. The wall of the cavity is about two cells thick and the germ gland is clearly defined containing both single germ cells and balls of several cells. The pharynx in this form is also set back from the anterior end.

The largest rediae (Fig. 52) are all rounded at their posterior extremities and their body cavities are very large with thin walls. The germ gland is much reduced. At one side near the anterior end is located the birth pore with protruding lips. The rediae vary in size up to the largest measured which is 0.73 mm. in length. The largest ones have from 25 to 30 germ balls of about the same size in their body cavities. The intestine is smaller in proportion to the size of the body but of about the same absolute size as in the smaller forms, and the oral sucker is very clearly set back from the anterior end. The outer layers at the anterior part are wrinkled so that the appearance is given of a series of horizontal folds from the anterior tip back to the middle of the body.

Besides the large rediae with the body cavity full of germ balls there are present numbers of large rediae with few or no germ balls and much constricted and twisted.

That these rediae are the nurse generations of *Cercaria trigonura* is very probable from their being found in every instance with that form. All the most immature rediae are about the same size and appear to belong to the same brood, yet there is no evidence as to their origin. Neither is there any evidence where the cercariae free in the tissues come from, for in none of the rediae can cercariae be distinguished. The old rediae shells may have been the nurses of these cercariae and rediae but even when a few embryos are found in these, they are merely large little differentiated germ balls. It is possible that in these snails

were represented several infections and that the approach of winter, for the examinations were made in November, may have arrested the development of the second brood.

The only possible group in Lühe's (1909) classification of the cercariae where *Cercaria trigonura* might fit is with the Microcercous cercariae. An analysis of the forms coming under this category shows that they cannot form a natural group. Dollfuss (1914) in the preliminary account of his work on this group separates from it the Cotylocercous cercariae which he considers to be a natural subdivision.

He gives the following characters for the Cotylocercous cercariae.

1. Cercariae developing in simple sporocysts parasitic in marine gastropods.

2. Oral sucker with stylet; stylet glands fill a large part of the anterior region of the body.

3. Bladder large not bifurcate occupying almost all the posterior region of the body; wall formed by a single layer of large granular cells, which have the appearance of glands.

4. Tail very short, wide at least at its base, consisting of a cup with thick walls of large cells, which functions as a sucker.

Dollfuss is in doubt in regard to the specific distinctness of some of the members of this group. He therefore designates them together provisionally under the name *Cercaria pachycerca* Diesing "sensu lato et var." Under this designation he includes *Cercaria brachyura* Lespes, *Cercaria cotylura* Pagenstecker, and several new forms. Besides these are included in the Cotylocercous cercariae as undoubtedly distinct species *Cercaria linearis* Lespes and *Cercaria buccini* sp. inq. Lebour. Dollfuss states in regard to this group that the cercariae are so alike in structure that the adults must be closely related.

Aside from the cercaria of *Catoptroides macrocotyle* Lühe *(Phyllodistomum folium* Ssinitzin*)* and metacercariae, which have been related to the Microcercous cercariae without any good reason, there are left after the separation of the Cotylocercous cercariae, five more or less well known forms.

1. *Cercaria limacis* (Moulinie' (1856:83, 163-164) from sporocysts in the terrestrial molluscs *Arion rufus L.* and *Limax cinereus* O. F. Müller.

2. *Cercaria micrura* de Filippi (1857:5-7) (larva of *Sphaerostomum bramae* (O. F. Müller) from sporocysts in the freshwater snail *Bithynia tentaculata.*

3. *Cercaria myzura* Pagenstecher (1881:25-26) from rediae in the fresh-water mollucs *Neritina (Theodocia) fluvialvis* L.

4. *Cercaria trigonura* mihi from rediae in the fresh-water snail *Campeloma subsolidum.*

5. *Cercaria columbellae* Pagenstecher (1862:305-306) from rediae in the marine mollucs *Columbella rustica* L.

Of the two of the above cercariae developed in sporocysts only *Cercaria micrura* agrees in structure with the characters given for the Cotylocercous cercariae. The only reason for not including it in this group is apparently that it is a fresh-water form. Just why it should be excluded from this group for this reason when it agrees with them in structure is not clear.

Cercaria myzura Pagenstecher, *Cercaria columbellae* Pagenstecher, and *Cercaria trigonura* mihi are the three stumpy-tailed forms which develop from rediae. Two are from fresh-water and one is marine. Both of Pagenstecher's forms are so insufficiently known that but little structural comparison is possible. *Cercaria myzura* and *Cercaria columbellae* both have the truncated tail like Cotylocercous group.

Cercaria trigonura is unique among the stumpy-tailed forms in having a large posterior gland opening at the base of the tail and a bicornuate excretory vesicle. It differs from all except Moulinie's (1856:-83, 163-164) *Cercaria limacis* in having a blunted tail, which is not modified as a sucker.

FURCOCERCOUS CERCARIAE

Sporocysts containing small forked-tailed cercariae with eye-spots, were found in five out of thirty-eight specimens of *Lymnaea reflexa* from a small pond in the suburbs of Chicago, Illinois. I propose to name this form *Cercaria douthitti.*

The livers of the snails infected with *Cercaria douthitti* were filled with a tangled mass of elongate, cylindrical sporocysts. The walls of the sporocysts were so thin and in such close contact with the liver lobes (Fig. 63, sw), that it was impossible to free individual sporocysts and to follow them to any length. They were irregular tubes of varying caliber, had no free, mobile, club-shaped ends sticking out, and were filled with large numbers of embryos in various stages of development. (Fig. 64). The walls of the sporocysts were made up of a very thin fibrous layer on the inside of which were scattered nuclei (Fig 63).

None of the cercariae were found outside of the sporocysts in the snail, but when the liver was dissected large numbers worked their way out. Their progress from place to place was quite erratic altho they moved their bodies and tails vigorously. When in locomotion the body and tail were both somewhat contracted and both moved back and forth.

The movement of the tail was not a lashing as in many forms, but a vibration in which the middle region was the most active. The cercaria kept catching hold with its acetabulum and extending its anterior end, but was not able to take hold with the oral sucker, which even in the older specimens was not fully developed. Sometimes when a cercaria under observation was pressed lightly with a cover-glass it would catch hold with the ventral sucker and the vibrations of the tail would cause it to swing round and round on the sucker as pivot.

Cercaria douthitti is a very small form, cylindrical in cross section, slightly wider at the center and tapering from the acetabulum to the posterior end to a width equal to about that of the tail. The body has an average length in well extended mounted specimens of 0.19 mm. and a width of 0.067 mm. The tail is bifid and even when contracted is equal to about one and one-half the length of the body. The lobes form less than one-third of its length and are definitely constricted from the main portion, making the tail appear as if jointed (Fig. 55). The main stem of the tail has an average length of 0.22 mm. and a width of 0.025 mm., while the lobes have about half that width and an average length of 0.089 mm. When the cercaria is alive the tail has a range of variation from less than once to about twice the length of the body. Underneath the thin cuticula and the muscle layers of the tail is a layer of unicellular club-shaped glands(?), which lie close together and have their ducts extending forward to open to the outside along the sides. These glands were only seen in the living specimens. The central core of the tail is composed of parenchymatous tissue, thru which flows the caudal branch of the excretory system. The base of the tail fits into a depression at the posterior end of the body, which is open ventrally (Fig. 57).

The oral sucker of *Cercaria douthitti* is proportionally large, measuring on the average 0.057 mm. in length and 0.045 mm. in width. It is a mass of embryonic cells which are separated from the surrounding tissue by a fibrous sheath, except that the ducts of the cephalic glands pass thru to open at the anterior tip. There is no differentiation into muscle fibers and no mouth or oral cavity is marked. *Cercaria ocellata,* a European forked-tailed form which corresponds in structure very closely to *Cercaria douthitti* is described as having a definite mouth opening, by La Valette St. George (1855:22-23). He also gives measurements much smaller for the oral suckers than those of *Cercaria douthitti,* making it less than half as large as the acetabulum (0.013 mm. to 0.033 mm.) Lühe (1909:206) questions his measurements, and since in La Valette St. George's drawing that region is not clear, it may well be that he did not grasp the true proportions of the oral sucker, and that it is as

large in his form as in *Cercaria douthitti*. The acetabulum is fully functional as noted above. It is very small, on the average 0.025 mm. in diameter, situated just back of the middle of the body.

The eye-spots are in front of the middle of the body and located nearer the dorsal side. The pigment masses which compose them are in the shape of concavo-convex discs, 0.007 mm. in diameter, placed so that the concave surfaces are toward the sides of the body. Fitting into the concave side of each is a small lens. In the region of the eyes and lying just ventrad and behind them is the central nervous system. A cross section of the cercaria in the region of the eye-spots brings out these relations clearly (Fig. 56, e).

The region back of the center of the body of *Cercaria douthitti* is almost completely filled with large unicellular cephalic glands, the usual number of which is eight. The most anterior reach to the middle of the body and from all, large ducts extend forward in two groups. These two groups of ducts pass thru the sheath of the oral sucker posteriorly and traverse this organ to open at the anterior tip of the body (Fig. 59, 60, 61, 62). No cephalic spine is present altho these glands appear to be analogous to stylet glands. *Cercaria ocellata* La Valette St. George (1855:22-23) is the only other furcocercous cercaria in which such glands are described. The glands are flasked-shaped and have a length varying from 0.04 mm to 0.05 mm. and a width of from 0.025 to 0.03 mm. The thickness is about equal to the width. A traverse section (Fig. 58) thru the acetabular region of *Cercaria douthitti* shows how much of the body space is taken up by the cephalic glands.

At the posterior end of the body of *Cercaria douthitti* is a small excretory vesicle from which two crura could be traced forward only as far as the acetabulum. Backward from the bladder two small vessels pass into the tail (Fig. 57, ex). These soon unite into the central caudal vessel which divides to run down the lobes and opens at their tips (Fig. 55). No concretions of any kind were present in the excretory system.

Just in front of the excretory bladder and wedged between the tips of the cephalic glands, is a small mass of nuclei the anlagen of the reproductive organs.

The furcocercous or forked-tailed cercariae are very imperfectly known. The anatomy of only a few of the known forms is at all well worked out and the life-history of no one of them has been determined. At least a dozen species have been reported as distinct, some of which, however, have been described very briefly in the older accounts. Sufficient evidence is not available to justify any conclusion as to the natural or artificial character of this group.

Only one of the forked-tailed cercariae, *Cercaria ocellata* La Valette St. George corresponds at all closely in structure to *Cercaria douthitti.* The structure of this form has been fairly well worked out by La Valette St. George (1855:22-23) and Moulinié (1856:172-173). *Cercaria ocellata* agrees with *Cercaria douthitti* in the large unicellular glands of the posterior body region, in the presence of eyespots, in the length and jointed character of the tail, and in fact that the forked portion is only one-third of its total length. The ratio in size of the suckers may agree as stated above.

Cercaria ocellata differs in several particulars from *Cercaria douthitti.* The former is almost twice as large, is found in a different host, in a different continent, and has narrow fin-like extensions on the divided lobes of the tail.

No suggestion can be made as to the life-history of *Cercaria douthitti.* Its structure is such as not even to suggest to what family of distomes the adult belongs. In fact hardly a suggestion has been made in regard to the life-histories of the forked-tailed cercariae and no experiments that I can find have been carried on to trace their development. Certainly further studies are needed on their structure and development.

XIPHIDIOCERCARIAE

Lühe (1909:189) defines Diesing's (1855) group of the Xiphidiocercariae or stylet cercariae as follows:

Slender-tailed distome cercariae with a boring spine on the rounded anterior end. Eyes lacking; develop in sporocysts; encystment in a secondary intermediate host.

Since this group is formed on likenesses in but few larval characters it can be considered only within wide limits as expressing relationship. On account of their small size and also since many of them are known only from the older accounts many of the forms of this group are very insufficiently described. Five new forms are added to this group by the study of my material. In the following account the new American forms will be compared with the most closely related of the already known species, and where it is possible an attempt will be made to fit them into natural groups.

Two of these forms with the related European species agree so closely in structure that a new group, the Polyadenous cercariae will be formed for them.

POLYADENOUS CERCARIAE

In eighteen per cent., of 170 specimens of *Planorbis trivolvis* collected from the drainage ditch north-east of Urbana, Illinois, the livers were filled with elongate, cylindrical sporocysts very much twisted together. The sporocysts were not branching but it was very difficut to trace out the individual sacs. When this could be done they were found to be of about uniform caliber and various lengths (Fig. 66). Two that were measured were 1.48 mm. and 1.9 mm. in length and varied in diameter from 0.13 mm. to 0.17 mm. The walls were thin and contained flecks of orange pigment, which were very dense in the oldest specimens. Many of the sporocysts contained large numbers of actively moving cercariae which would escape and swim about freely when the liver was teased apart. The wall of the sporocyst was composed of a layer of pavement epithelium with flattened nuclei. No thickenings were found in the wall and no traces of germ gland, altho small germ balls were free in the cavity. Cercariae at all stages of development were found in the sporocysts (Fig. 65). I propose to call this species *Cercaria isocotylea* from the fact that the acetabulum and the oral sucker are very nearly equal in size.

Cercaria isocotylea (Fig. 68) is oval elongate, slightly pointed anteriorly, and of uniform width from the region of the pharynx back to the acetabulum. The length and the width varied with the contraction state within rather wide limits. From the measurements of mounted specimens of moderate contraction, the length averages 0.17 mm. and the width 0.06 mm. The cross section is oval and the thickness a little greater than half the width. The tail is small in proportion to the size of the body and set in a groove on the ventral side of the posterior end. When contracted it may be less than one-half the body length, but when the cercariae is swimming it may be extended to greater than that length. Under ordinary circumstances it has an average length of 0.01 mm. and a width at its base of 0.02 mm.

Cercaria isocotylea moved actively both in open water and on a substratum. When swimming it turned so that the ventral side was up, the body was contracted and bent slightly ventrad. The tail became much extended and lashed rapidly backward and forward. It did not however have the power of moving the animal definitely in one direction for any length of time, and locomotion was very erratic. Whenever while swimming the cercaria came in contact with a surface, the tail ceased its lashing and the body began to stretch and reach around until the oral sucker could obtain a hold. Then the animal would creep along with the aid of its suckers. Sometimes after the cercariae had come

in contact with a surface and extended its body, the tail resumed its lashings and swimming was started again with the body extended. This was simply preliminary to the contraction of the body and the resumption of the usual swimming position.

The oral sucker of *Cercaria isocotylea* (Fig. 68, os) has an average length in mounted sections of 0.04 mm. and a width of 0.037 mm., while the acetabulum which is spherical in the living animal, is about two-thirds of the distance from the anterior to the posterior end and has a diameter of 0.036 mm.

Set in the dorsal wall of the oral sucker is a large sylet (Fig. 67) which is sharp pointed and has a thickening two-thirds of the distance from its base to its tip. It is flattened ventrally, has a length of from 0.028 mm. to 0.030 mm. and a width at its base one-sixth of its length.

The whole surface of the body back to the anterior margin of the acetabulum is thickly set with tiny cuticular spines which are 0.003 mm. to 0.004 mm. in length. Back of this region the cuticula is entirely smooth.

On each side of the stylet open the ducts of the stylet glands, which form a group on each side. The glands are elongate, sac-shaped, unicellular and faintly granular, with a length of from 0.02 to 0.025 mm. and a width of from 0.011 to 0.013 mm. They form two clumps of from six to eight in a clump, in the region just in front and to each side of the oral sucker.

In this stage of development of the cercariae no cystogenous glands are present.

Except for the mouth, oral cavity, very short prepharynx, and pharynx the digestive system of *Cercaria isocotylea* is undeveloped. The mouth is very small having a transverse diameter of 0.012 mm. and the round pharynx is 0.016 mm. in width.

The excretory pore opens on the dorsal side just at the base of the tail. The bladder is bicornuate consisting of a median part and two lateral horns which reach on each side up to the middle of the acetabulum. From the anterior and posterior regions on each side can be traced small vessels which unite into a short common duct to open at the tips of the horns. (Fig. 68, ex)

The anlage of the reproductive organs is not divided into definite parts. It consists of a mass of small nuclei which lies dorsad and just in front of the anterior margin of the acetabulum. This connects with a larger mass which is dorsal to the posterior part of the acetabulum by a broad band running around dorsal to the left margin of the sucker.

Among the specimens of *Lymnaea reflexa* from Chicago was one which contained a number of elongated unpigmented sporocysts, which

were found in the liver with the rediae of *Cercaria reflexae.* These sporocysts were much like those of *Cercaria isocotylea,* and were so thin walled and so closely interwoven with the lobes of the liver that none were isolated for accurate measurements. Altho large numbers of the cercariae in the sporocysts were mature, few were free in the liver of the host. When, however, the liver was taken out of the snail many were freed and swam actively about. I propose the name *Cercaria polyadena* for this species from the fact that the body of the cercaria contains such large numbers of gland cells.

The position of *Cercaria polyadena* in swimming was similar to that of *Cercaria isocotylea.* The tail was, however, somewhat stronger than in the latter species and the animal was able to move forward definitely and fairly rapidly. Whenever the cercaria came in contact with a surface, it immediately settled down, took hold with its suckers, and crept along.

The tail was very easily detached from the body and would continue swimming for some time with a wriggling motion. Whenever an actively detached tail came in contact with the substratum, it ceased wriggling and alternately extended and contracted as if it were still attached to a living cercaria. One of the detached tails kept up active movement for over fifteen minutes and then was stopped by the drying up of the water around it.

Small thin walled cyst containing tailless individuals of *Cercaria polyadena* were found scattered in with the material preserved for study (Fig. 71). It is probable that these cysts were formed after the liver was removed from the snail, and that *Lymnaea reflexa* is not the secondary intermediate host of this species. The formation of the cyst was not observed but that the glands were ready for secretion is shown by the fact that the extrusion of the cystogenous material was observed in one individual that was flattened under a cover slip. The cysts were round and varied in diameter from 0.15 mm. to 0.16 mm., and the transparent cyst wall varied in thickness from 0.005 to 0.007 mm.

Cercaria polyadena (Fig. 70) is very variable in shape, living specimens changing from 0.12 mm. when contracted to 0.30 mm. at greatest extension. When most contracted the tail may be less than one-half the body length, but when the animal was swimming it reaches to 0.30 mm. The average measurements of five mounted individuals in about the state of contraction of the figure, give the length of 0.18 mm., the width of 0.07 mm., the length of the tail 0.12 mm. and its width 0.017 mm. The tail is attached in a groove on the ventral surface of the posterior end, and altho it is small for the size of the body it is relatively larger than in *Cercaria isocotylea.*

The oral sucker has an average diameter in mounted specimens of 0.040 mm. and the spherical acetabulum which is three-fifths of the distance from the anterior to the posterior end is 0.025 mm. wide.

In the dorsal wall of the oral sucker is set a stylet like that of *Cercaria isocotylea.* It is 0.028 to 0.03 mm. in length and thickened as in the other species.

The whole surface of the body is set with tiny spines contained entirely within the cuticula and not set in rows; these thin out somewhat in the postacetabular region.

Two groups of voluminous ducts pass up dorsad to the oral sucker from the stylet glands, which fill most of the space from the acetabulum to the pharynx. The diameter of one of these ducts is from 0.004 mm. to 0.005 mm. The stylet glands are divided into two groups of from ten to twelve in a group, and the individual glands vary in length from 0.017 to 0.022 mm., and in width from 0.010 mm. to 0.014 mm.

Cystogenous glands are present both on the dorsal and ventral sides of the body from the pharynx to the posterior end.

In *Cercaria polyadena* the oral cavity is followed by a short prepharynx 0.015 mm. in diameter. No traces were seen either of the esophagus or the intestinal ceca.

The excretory bladder is bicornuate and the excretory pore is located dorsally at the base of the tail. The two horns of the vesicle extend up to the posterior lateral margins of the acetabulum, and each receives a small vessel. This receives a long vessel from the region of the pharynx and a short vessel from the posterior end. The lining of the vesicle is formed of a layer of slightly flattened cuboidal epithelial cells with prominent nuclei and well defined cell boundaries.

The anlage of the reproductive organs is not differentiated into its individual parts. It is represented by an elongate s-shaped mass of nuclei lying dorsad to the acetabulum and extending backward beyond its posterior margin.

Cercaria polyadena and *Cercaria isocotylea* are very much alike and form the nucleus of a group the members of which present such uniformity of characters that they must be considered to be related. The name Polyadenous cercariae may then be proposed as the name of a natural group the members of which correspond closely to *Cercaria polyadena.*

The following are the characters of the Polyadena cercariae:

1. Development in gastropods in elongate sac-shaped sporocysts.
2. Tail slender and less than the body length except when very much extended.

3. Acetabulum back of the middle of the body and smaller than the oral sucker.

4. Stylet about 0.030 mm. in length, six times as long as broad, and with a thickening one-third of the distance from the point to the base.

5. Stylet glands, six or more on each side between the acetabulum and the pharynx.

6. Excretory bladder bicornuate.

7. Very short prepharynx and small pharynx present. Esophagus when developed short to of medium length. Intestinal ceca (when present reaching to posterior end of body).

Two European fresh-water cercariae, *Cercaria limnaeae ovatae* von Linstow and *Cercaria secunda* Ssinitzin, without doubt belong to this group. They both agree in all known particulars with the characterization given above. No mention is made, however, in von Linstow's (1884) account of stylet glands.

There are definite specific differences between the four forms which constitute the Polyadenous cercariae. Of the two American forms *Cercaria polyadena* has a larger body and tail, a smaller oral sucker, and a larger number of stylet glands. *Cercaria limnaeae ovatae* is the largest of the group, has much larger suckers than any of the others, and is developed in larger sporocysts. The closest correspondence is between *Cercaria polyadena* and *Cercaria secunda* Ssinitzin. These two species are certainly very closely related. *Cercaria secunda* is, however, larger in size and has slightly larger suckers and fewer stylet glands than *Cercaria polyadena.*

Some suggestion can be made in regard to the type of adults into which the cercaria of this group develop. *Cercaria limnaeae ovatae* has been assigned to *Opisthioglyphe rastellus* (Lühe, 1909:108) and Ssinitzin (1905) suggests that *Cercaria secunda* may be the larva of a *Plagiorchis species.* It would seem probable from the above facts and the structure of the excretory and digestive systems that the Polyadenous cercariae belong in Lühe's subfamily *Plagiorchiinae* which contains *Opisthioglyple* as well as *Plagiorchis.* The further development of the two American forms is entirely unkown.

CERCARIAE ORNATAE

In 5 per cent. of the specimens of *Physa gyrina* from Rockford, Illinois, the body contained a tangled mass of elongated, orange pigmented sporocysts. The tubes did not branch, they were of varying

caliber and club-shaped ends protruded from the mass. They were very much twisted together and none of the individual sacs were disentangled without breaking. The jutting ends moved slightly, swaying backward and forward.

Thruout their whole length the sporocysts (Fig. 77) were stuffed with cercariae of different ages, and mature forms in large numbers wormed out of the broken places in the sporocysts. The swimming movement of the cercaria offered nothing peculiar and since the oral sucker did not appear to function, creeping was not very effective. The name *Cercaria hemilophura* is proposed from the fact that a fin-like projection extends for half the length of the tail.

Cercaria hemilophura (Fig. 76) is oval elongate in shape and widest at about the middle. The average length in well extended mounted specimens is 0.38 mm. and the width 0.14 mm., with a thickness of about one-half the width.

The tail at average extension is about the length of the body, 0.36 mm. being the average in toto mounts and with a width of 0.048 mm., but it can be extended to almost twice that length. Along the ventral surface of the posterior half of the tail extends a fin-like projection, which at its widest is about half the width of the tail.

The oral sucker has a length of 0.065 mm. and the acetabulum, which is just back of the middle of the body, has a diameter of 0.049 mm.

The stylet (Fig. 75) is small, tapers regularly to a point and has no thickened region. It measures 0.020 mm. in length and 0.005 mm. in width at its base.

The whole surface of the body is covered with very small cuticular spines pointing backward, which are very dense in the preacetabular region but thin out slightly posteriorly. They are contained entirely within the thickness of the cuticula and have a length of from 0.0055 mm. to 0.0065 mm.

The whole body contains large numbers of small cystogenous glands filling almost all the available space.

Stylet glands could not be distinguished.

The digestive system of *Cercaria hemilophura* is very clearly differentiated. The oral cavity is followed by a very short prepharynx and a good sized pharynx 0.033 mm. in diameter. From the pharynx a large esophagus reaches back almost to the acetabulum. The esophagus is thin walled but the intestinal ceca are lined with cuboidal cells which at this stage fill most of the lumina.

It was possible in many cases to trace the branches of the excretory system to the flame cells. The bladder is club-shaped, extending about three-fourths of the distance from the posterior end to the acetabulum,

and widens slightly at its anterior end. Into it flow two vessels from the region of the oral sucker on each side, which are met by vessels from the posterior end at the region of the acetabulum. Small branches lead from the flame cells and connect with these branches. Figure 76 shows the excretory system of *Cercaria hemilophura.*

The anlagen of the reproductive organs are represented by a two lobed mass of nuclei dorsal to the acetabulum.

According to Lühe's classification of the Xiphidiocercariae *Cercaria hemilophura* would belong with the group *Cercariae ornatae.* He gives the following definition for this group:

''Distome Cercarien mit Bohrstachel, deren schlanker Ruderschwanz einen Flossensaum besitzt.''

He included in this group *Cercaria ornata* La Valette and *Cercaria prima* Ssinitzin. This is certainly not a natural subdivision, since the three forms are very different in other structures. The presence of such a character as the ''Flossensaum'' hardly forms the basis for a natural group. Since it has been developed also in such widely different groups as the monostomes and the echinostomes. At the present state of our knowledge it seems impossible to relate *Cercaria hemilophura* to any natural group. Neither is there any suggestion as to the further development of this species.

MICROCOTYLOUS CERCARIAE

The tissue above the gills in three out of thirty-six specimens of *Campeloma subsolidum* from Hartford, Conn., was heavily infected with oval thin-walled sporocysts. The sporocysts had granular, somewhat opaque walls, varied in shape from almost round to elongate oval, and contained small cercariae in different stages of development. None of the cercariae were fully mature and none were found free in the tissues of the host. There was little movement of the cercariae either within the sporocysts or when freed. I propose the name *Cercaria leptacantha* for this species on account of the small size of the stylet.

The sporocysts (Fig. 81) varied from 0.26 mm. to 0.41 mm. in length and from 0.15 mm. to 0.26 mm. in width.

The body of *Cercaria leptacantha* (Fig. 80) is oval elongate and almost circular in cross-section. The average measurements of five well extended mounted specimens are 0.12 mm. in length and 0.063 mm. in width. The tail is not fully developed still remaining as a direct continuation of the body and having little power of movement. It is less than the length of the body and slender, averaging 0.081 mm. in length and 0.016 mm. at its greatest width.

In none of the individuals studied were the suckers fully developed or functional. The oral sucker shows a beginning of a mouth cavity but the acetabulum is merely a rounded off mass of embryonic nuclei. In mounted specimens the oral sucker averages 0.027 mm. in diameter and the acetabulum, which is back of the middle of the body, has a width of 0.024 mm.

On the surface of living specimens of *Cercaria leptacantha* were scattered highly refractive round globules of different sizes, which appeared like water or oil droplets. These bodies, which resemble the concretions in the excretory systems of certain cercariae, were so prominent that they could be seen thru the walls of the sporocysts, but disappeared in the preservation of the material.

The small characteristic stylet (Fig. 79) is 0.011 mm. to 0.13 mm. in length, and 0.0025 mm. in thickness at its base.

Two kinds of glands were present in *Cercaria leptacantha*. The first type consists of small irregular shaped bodies with granular contents at the anterior lateral margins of the acetabulum. The other type are almost clear globlet shaped stylet glands, four on each side arranged along the body lateral to the acetabulum, with ducts from their outer margins leading up to the cephalic spine. No ducts were found for the first type of gland, but from their granular contents they may be cystogenous in character.

The digestive system of *Cercaria leptacantha* is represented only by a short prepharynx and a small pharynx 0.09 mm. in diameter.

Of the excretory system only the elongate, club-shaped bladder can be distinguished.

The anlage of the reproductive organs is represented merely by a large mass of small nuclei dorsal and posterior to the acetabulum.

Cercaria leptacantha belongs to a group of very small cercariae which Lühe (1909:196) calls Cercariae Microcotylae. It is possible that they form a natural group. They are, however, so insufficiently known that no final judgment can be passed on their relationships. At present it seems best to follow Lühe in considering them a provisional group, with *Cercaria microcotyla* Filippi as the type and the following characteristics.

1. Developed in gastropods in round or oval sporocysts which are seldom more than twice as long as wide.

2. Cercariae under 0.2 mm. in length.

3. Acetabulum back of the middle of the body and smaller than the oral sucker.

4. Stylet glands not more than four on each side and arranged in rows on each side of the acetabulum.

5. Digestive system undeveloped except for a short prepharynx and a small pharynx.

Three European and three Egyptian cercariae are sufficiently known to be included with any certainty in this group. The European forms are *Cercaria pugnax* La Valette, *Cercaria microcotyla* Filippi, and *Cercaria subulo* Pagenstecher (for description of these forms see Lühe, 1909:196-198), and the Egyptian forms are *Cercaria celluosa* sp. inq., *Cercaria pusilla* sp. inq., and *Cercaria exigua sp. inq.* all described by Looss (1896:227-232). Insufficiently known forms which from their small size and the shape of the sporocysts may belong to this group are *Cercaria chlorotica* Diesing, *Cercaria alba* Ercolani, and *Cercaria punctum* Ercolani. *Cercaria parva* Ercolani in which the oral sucker is smaller than the acetabulum agrees in its other characters with the members of this group.

The Microcotylous cercariae are best distinguished from each other by the size and shape of their stylets. *Cercaria leptacantha* agrees most closely with the Egyptian species *Cercaria exigua.* It is larger than this species however, the suckers differ in size and the ratio of size, and the stylets differ in size and shape.

Only one suggestion is found in regard to the adults of this group. Looss (1896:232) considers that the three cercariae of this type described by him may belong to some small distomes found in Egypt in the intestines of chameleons and lizards. He offers no particular grounds for this hypothesis.

Last will be considered a form of the Xiphidiocercariae which seems to be different from all forms previously described. The livers of three out of ninety-one specimens of *Physa anatina* from Manhattan, Kansas, were infected with sausage-shaped sporocysts (Fig. 72) which contained cercariae in different stages of development. I propose for this species the name *Cercaria brevicaeca* from the fact that the intestinal ceca are very short.

Cercaria brevicaeca moved clumsily and irregularly while swimming and did not creep by aid of its suckers. The infection was very slight and all the observations were made from living specimens. None of the cercariae were observed to live more than two or three hours after removal from the snail.

Cercaria brevicaeca (Fig. 74) was elongate oval in shape and its tail, which was very easily lost, had about the same length as the body. At average extension the body had a length of about 0.30 mm. and a width of 0.14 mm. The tail did not change its shape very greatly and ranged in length only from 0.22 mm. to 0.38 mm. with a width at its base of 0.038 mm. It was attached in a groove in the ventral side of the posterior end and when contracted had a tendency to curl at its tip.

The oral sucker of *Cercaria brevicaeca* had an average diameter of 0.082 mm. and the acetabulum, which is just back of the middle of the body, was slightly larger, 0.087 mm.

The stylet (Fig. 73) had a length of 0.018 mm. and was slightly thickened 0.007 mm. from its point.

The body back to the acetabulum was covered thickly with rows of very tiny spines.

In the region between the acetabulum and the pharynx were two clumps of from ten to twelve stylet glands, varying in length from 0.026 mm. to 0.035 mm. and in width from 0.018 mm. to 0.025 mm. The ducts from these glands united into two groups one on each side which passed dorsad of the oral sucker to open beside the stylet.

Almost every bit of available space behind the pharynx was filled with cystogenous glands, which from the surface appeared as round, granular bodies 0.014 mm. to 0.017 mm. in diameter.

The oral cavity was followed by a short prepharynx and a small pharynx, 0.030 mm. in diameter. The short, narrow esophagus divided just in front of the acetabulum into short intestinal ceca which did not reach beyond the acetabulum. The lumina of the ceca showed only as irregular, elongate spaces in the granular contents.

Of the excretory system only the peculiarly shaped vesicle could be made out. This was composed of a pyriform median portion, and two more narrow lateral parts which almost completely surrounded the acetabulum. The pore opened dorsad at the base of the tail.

No cercariae were found in the literature closely corresponding with *Cercaria brevicaeca*. Especially unique is the shape of the excretory vesicle.

THE CLASSIFICATION OF THE CERCARIAE

At the present state of our knowledge it is impossible to fit most of the cercariae into the general trematode classification, for, except in those forms like the echinostomes or the amphistomes, where the larvae are much like the adults, or in a group like the family *Gorgoderinidae*, where the life histories of several species have been worked out, little

is definitely known of the relation of the cercariae types to the adults. Therefore for convenience it has seemed advisable to build up a tentative classification of the cercariae, treating them almost as if they were an independent class of the animal kingdom. Of necessity such a classification must be based pretty largely on superficial characters. As our knowledge increases wherever possible natural groups must be substituted for the artificial, and as more and more larvae are connected with the adults, the classification of the cercariae will gradually be merged with that of the adults.

In order to understand clearly the classification that has been made for larval trematodes, a careful analysis of the characters used for comparison must be made. Cercarial characters can be roughly divided into two main groups: (1) adult characters, and (2) larval characters. By adult characters of a cercaria are meant those which foreshadow adult structure. It is by the use of these characters as a basis that the greatest progress in natural classification can be made, since the more the adult characters are developed, the more will the cercariae resemble the adults, as in amphistome and echinostome larvae. For example the digestive and the excretory systems of the cercariae of these groups are much like those of the adult. Sometimes in the larva definite specific peculiarities of the adult can be distinguished in detail. Thus Looss (1896:192-197) in attempting to prove by morphological comparison that *Monostomum verrucosum* Froel *(Notocotyle triseriale* Diesing) and *Cercaria imbricata* Looss belong to the same species, advances as his strongest argument, that in the mature cercaria are found around the excretory pore plications arranged as the rays of a circle like those found in the adult. A combination of adult characters will often give a clue to the family or even in a few cases to the genus to which the cercaria belongs. Allowance must be made however for the fact that adult characters may be somewhat modified in the development of the cercaria. For example the loss of the tail modifies the excretory system, and changes in shape and proportion of the body change considerably the relative lengths of the different parts of the digestive system.

Larval characters of cercariae may be defined as those which are not carried over into adult life. Many structures are developed to meet the exigencies of larval conditions, and are merely temporary. In many cercariae much dependence must be placed on such characters in classification, for often as in the forked-tailed and stylet cercariae, adult characters are very little differentiated and the whole structure is very largely dominated by larval characteristics. This brings up the question as to how far such characters can be considered as expressing relationship. Like structures in cercariae either show relationship or

convergence due to adaptations to similar environments. Such an adaptation as the development of a boring spine which occurs in cercariae widely different in other characters, can hardly be considered as showing close relationship. When, however, cercariae are very similar in a number of larval characters such likeness can hardly be ascribed to convergence, and even if adult characters are not sufficiently developed for comparison, such forms can with reasonable certainty be placed together in natural groups.

Another question which must be considered in classifying certain cercariae, is whether the larvae of closely related adults might not be different on account of modifications in larval life. From consideration of conditions in other groups this would seem very possible. The little evidence that we have, however, seems to indicate that the cercariae of closely related forms are more alike than the adults. Lühe (1909:175) suggests this as one reason for the small numbers of cercariae known in comparison with the adults.

"Vielfach sint übrigens die Cercarien verschiedener Trematoden-Arten einander so ausserordentlich ähnlich, dass ihre sichere Bestimmung, wenigstens bei unseren jetztigen Kenntnissen, nicht möglich ist, and manche alte Art-namen haben dadurch die Bedeutung von Gruppen-statt von Artbezeichnungen gewonnen."

The statement of these problems shows how merely tentative at the present state of our knowledge must be considered any classification of cercariae.

The most extensive classification of the cercariae is that of Lühe (1909:173-210). His main subdivisions are for the most part based on the recognition of the relationship of the cercariae to the larger recognized adult groups. In the subdivision of the distome cercariae, however, his classification is to a considerable extent purely artificial, being based on the character of the tail. A summary of Lühe's classification follows.

LUHE'S CLASSIFICATION OF THE CERCARIAE

A. Lophocercariae
   Cercariae with longitudinal projections along the sides of the body. Ex. *Cercaria crista* La Valette.

B. Gasterostome cercariae
   Two long projections from the end of the body. Mouth opening in the middle of the ventral surface. Intestine simple sac-shaped. Ex. *Bucephalus polymorphus* Baer.

C. Monostome cercariae
   Ventral sucker lacking. Ex. *Cercaria urbanensis* Cort.

D. Amphistome cercariae
   Ventral sucker at the posterior end of the body. Ex. *Cercaria inhabilis* Cort

E. Distome cercariae
   Ventral sucker some distance in front of the posterior end of the body.
   1. Cystocercous cercariae
      Base of the tail forms a space into which the body can be drawn. Ex. *Cercaria macrocerca* Filippi.
   2. Rhopalocercous cercariae
      Tail having as great or greater width than the body. Ex. *Cercaria isopori* Looss.
   3. Leptocercous cercariae
      Tail straight, slender, and narrower than the body.
      a. Gymnocephalous cercariae
         Anterior end rounded, without stylet or boring spine. Ex. *Cercaria megalura* Cort.
      b. Echinostome cercariae
         Anterior end with a collar and crown of spines. Ex. *Cercaria trivolvis* Cort
      c. Xiphidiocercariae
         Anterior end with stylet. Ex. *Cercaria isocotylea* Cort.
   4. Trichocercous cercariae
      Tail set with spines. Ex. *Cercaria setifera* Moulinié.
   5. Furcocercous cercariae
      Tail forked at its end. Ex. *Cercaria douthitti* Cort.
   6. Microcercous cercariae
      Tail stumpy. Ex. *Cercaria brachyura* Lespés.
   7. Cercariaeae
      Tail entirely undeveloped. Ex. *Leucochloridium paradoxum* Carus.
   8. Rattenkönigcercariae
      Cercariae with tails joined, forming a sort of colony.

In the present state of our knowledge it seems to me that for the comparison of forms, no general grouping can be suggested which will be of more help to workers. It must be recognized, however, that many of the groups are purely artificial.. The Gymnocephalous cercariae have little in common but negative characters, and the stylet cercariae form a very heterogeneous mass. These and other groups are merely temporary arrangements for convenience and must be split up or rearranged into more natural groups as soon as our knowledge permits.

Marie Lebour (1912) tried to substitute for Lühe's classification one based on other characters. According to her classification the cercariae are divided into two large groups depending on whether they develop in rediae or sporocysts, and within these groups are formed small groups of apparently related forms. As an attempt to form closely related groups this work is very suggestive, but as a working classification it has very limited value. In the first place there is little evidence for the belief that development in sporocysts or rediae expresses fundamental relationship. Such widely divergent forms develop from sporocysts as *Bucephalus,* tailless cercariae, stylet cercariae, etc. The most important part of Miss Lebour's work is her attempt to build up natural groups of closely related forms centering around some well known species, as for instance, her *Spelotrema* group centering around *Spelotrema excellens.* The following is the essential part of Lebour's classification.

Lebour's Classification of the Cercariae

A. Gasterostomata
   Cercariae develop in sporocysts. Mouth at middle of ventral surface. Ex. *Bucephalous polymorphus* Baer.
B. Prostomata
   Mouth at anterior end.
   1. Distome cercariae
      Two suckers.
      a. Cercariae developed in sporocysts.
         (1) Gymnophallus group
            Cercaria tailless. Ex. *Cercaria glandosa* Lebour.
         (2) Fork-tailed cercariae
            Tail forked at its end. Ex. *Cercaria douthitti* Cort.
         (3) *Spelotrema* group
            Free swimming stage with stylet. Encysted cercaria tongue-shaped, covered with spines, with long prepharynx and esophagus, short ceca not reaching to the end of the body. Ex. *Cercaria* of *Spelotrema excellens.* (?)
         (4) Stumpy-tailed cercariae
            Tail broad and stumpy. Ex. *Cercaria brachyura* Lespés.
         (5) Lepodora group
            Body covered with spines. Intestinal ceca reaching nearly to posterior end of body. Tail

present in very young forms, but cast off before encystment, which takes place within the sausage-shaped sporocysts. Ex. Cercaria of *Lepodora rachiaea.* (?)

b. Cercariae developed in rediae.

(1) *Cercariae neptuneae*

Tail very thick and large, two eye-spots present. Excretory vesicle very thick walled. Ex. *Cercaria neptuneae* Lebour.

(2) *Acanthopsolus* group

Two eye-spots, intestinal ceca reaching nearly to the end of the body, thin tail developed in young forms but cast off before it is full grown. Ex. Cercaria of *Acanthopsolus lageniformis.* (?)

(3) Echinostomum group

Cercariae with anterior collar and crown of spines. Ex. *Cercaria trivolvis* Cort.

2. Monostome group

One sucker present. Ex. *Cercaria urbanensis* Cort.

It is in attempts to join a few closely related cercariae into groups which are probably natural, rather than in further broad generalizations which must be based on artificial characters, that hope for advance in the classification of cercariae lies. As more and more life-histories are worked out, such groups can be fitted into their place in the adult classification, until the relationship of all the cercariae groups to the adults will be known.

* *

Note. All of the species of Cercaria discussed in detail in this paper were originally described in my preliminary report (Cort, 1914).

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EXPLANATION OF PLATES

Unless otherwise stated all figures are drawn with a camera lucida.

The lettering on some toto drawings of the cercariae was omitted by error. The descriptions in the text will be sufficient to make the structure clear.

ABBREVIATIONS USED

ab	annular bands of muscle
ac	acetabulum
acr	anterior collar of redia
bp	birth pore of redia
cg	cystogenous glands
ccg	cephalic glands
cm	cystogenous material
cr	cercaria in redia
dc	ducts of cephalic glands
e	eye-spot
es	esophagus
ex	excretory system
exv	excretory vessel
gb	germ ball
i	intestinal cecum of cercaria
ir	intestine of redia
la	locomotor appendages of redia
lc	large central cells of tail
ls	lobes of snail's liver
ml	muscle layer
n	nervous tissue
os	oral sucker
p	pigmentation
pb	pharyngeal bulb
pc	parenchymatous cells
pl	pigment line
pr	pharynx of redia
ra	reproductive anlage
s	stylet
sc	cercaria in sporocysts
sg	stylet glands
sw	wall of sporocyst
vt	excretory vessels of tail

EXPLANATION OF PLATE

Figures 1 to 4. Free hand drawings of stages in the process of encystment of *Cercaria urbanensis*. X about 70.

Fig. 5. Mature *Cercaria urbanensis*, ventral view. Cystogenous glands not shown. X 140.

Fig. 6. Posterior locomotor projection of *Cercaria ephemera*. From Ssinitzin.

Fig. 7. Posterior locomotor projection of *Cercaria imbricata*. From Looss.

Fig. 8. Posterior locomotor projection of *Cercaria urbanensis*. X 433.

Fig. 9. Cross section of the tail of *Cercaria urbanensis*. X 433.

Fig. 10. Immature redia of *Cercaria urbanensis*.. X 88.

Fig. 11. Mature redia of *Cercaria urbanensis*. X 88.

Fig. 12. Mature redia of *Cercaria urbanensis*, showing constrictions. X 44.

Fig. 13. Cross section of immature redia of *Cercaria urbanensis*. X 433.

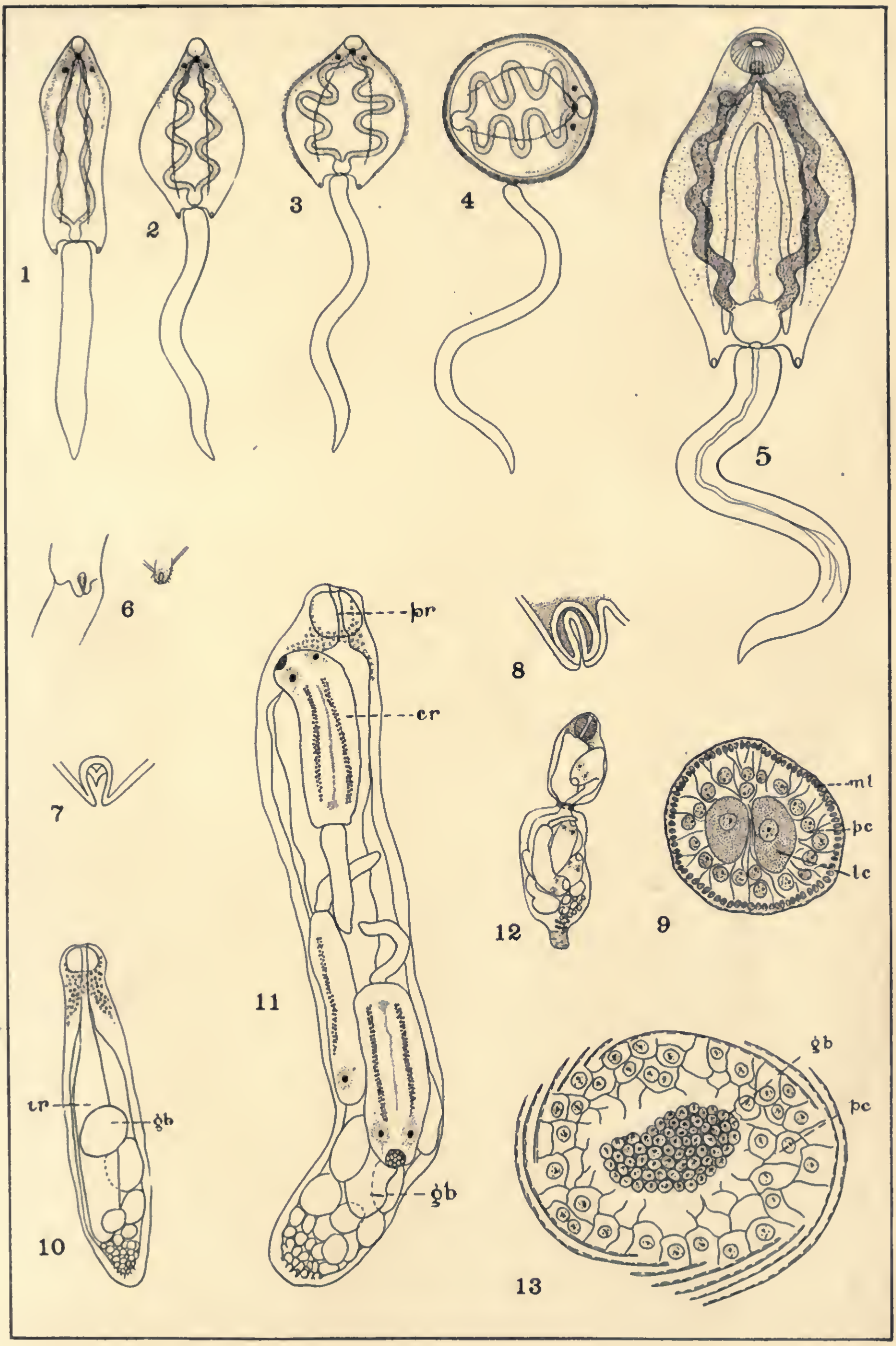

PLATE I

PLATE II

EXPLANATION OF PLATE

Fig. 14. Immature redia of *Cercaria urbanensis.* X 88.

Fig. 15. Redia of *Cercaria inhabilis.* X 88.

Fig. 16. Mature *Cercaria inhabilis,* ventral view. Cystogenous glands not shown. X 88.

Fig. 17. Cross section of *Cercaria inhabilis* in region of eye-spots. X 195.

Figures 18 to 21. Anterior body region of different stages of *Cercaria inhabilis,* showing changes in pigmentation. X 140.

Fig. 22. Cross section of the tail of *Cercaria inhabilis.* X 433.

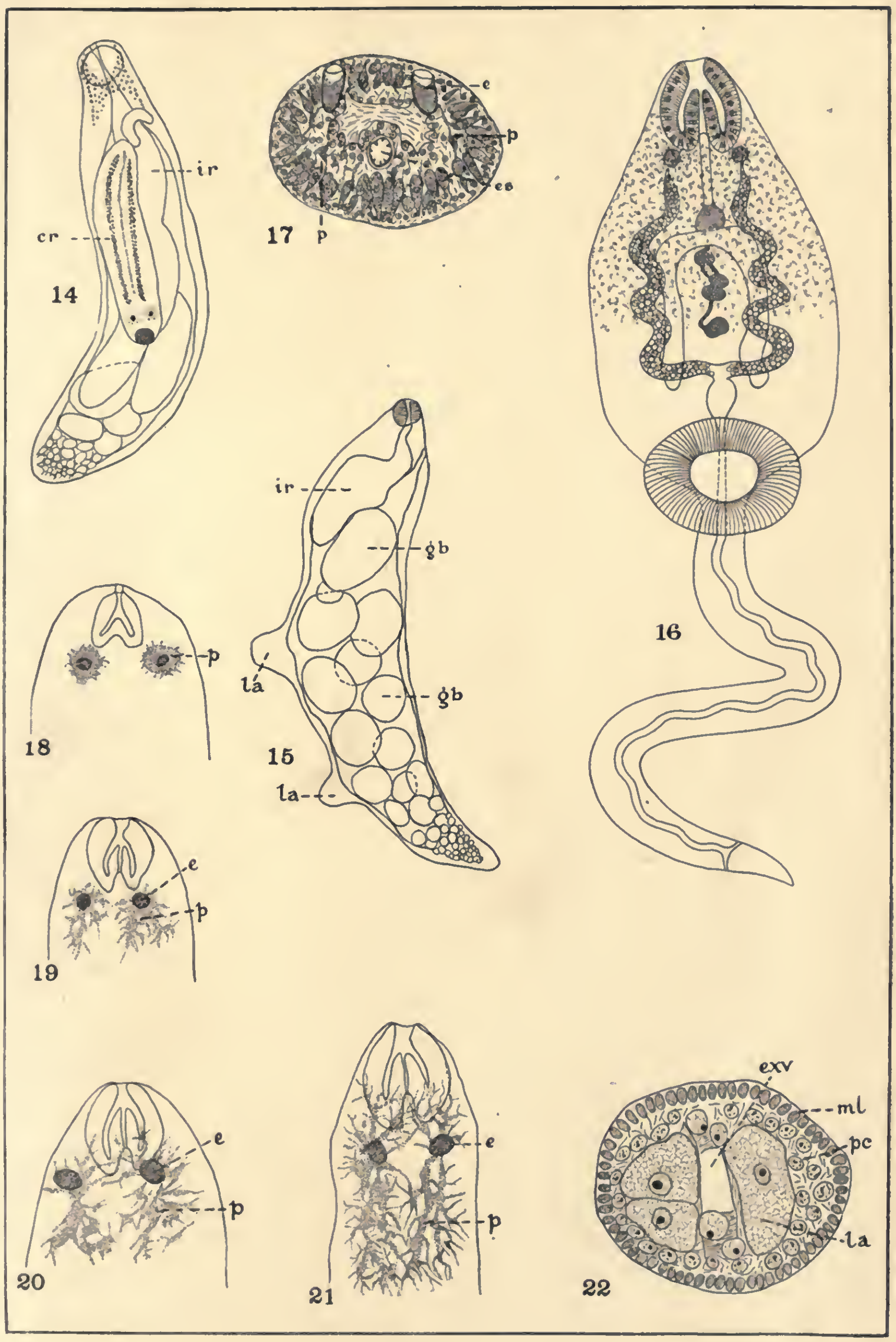

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PLATE II

PLATE III

EXPLANATION OF PLATE

Fig. 23. Mature *Cercaria diastropha,* dorsal view. Cystogenous glands not shown. X 88.

Fig. 24. Free hand drawing of *Cercaria diastropha* from the side. X 75.

Fig. 25. Redia of *Cercaria diastropha.* X 88.

Fig. 26. *Cercaria caryi,* ventral view. From Cary's material. X 140.

Fig. 27. *Cercaria megalura,* ventral view. From Cary's material. X 140.

Fig. 28. *Diplodiscus temporatus,* ventral view. From Cary's experimental tadpoles. X 140.

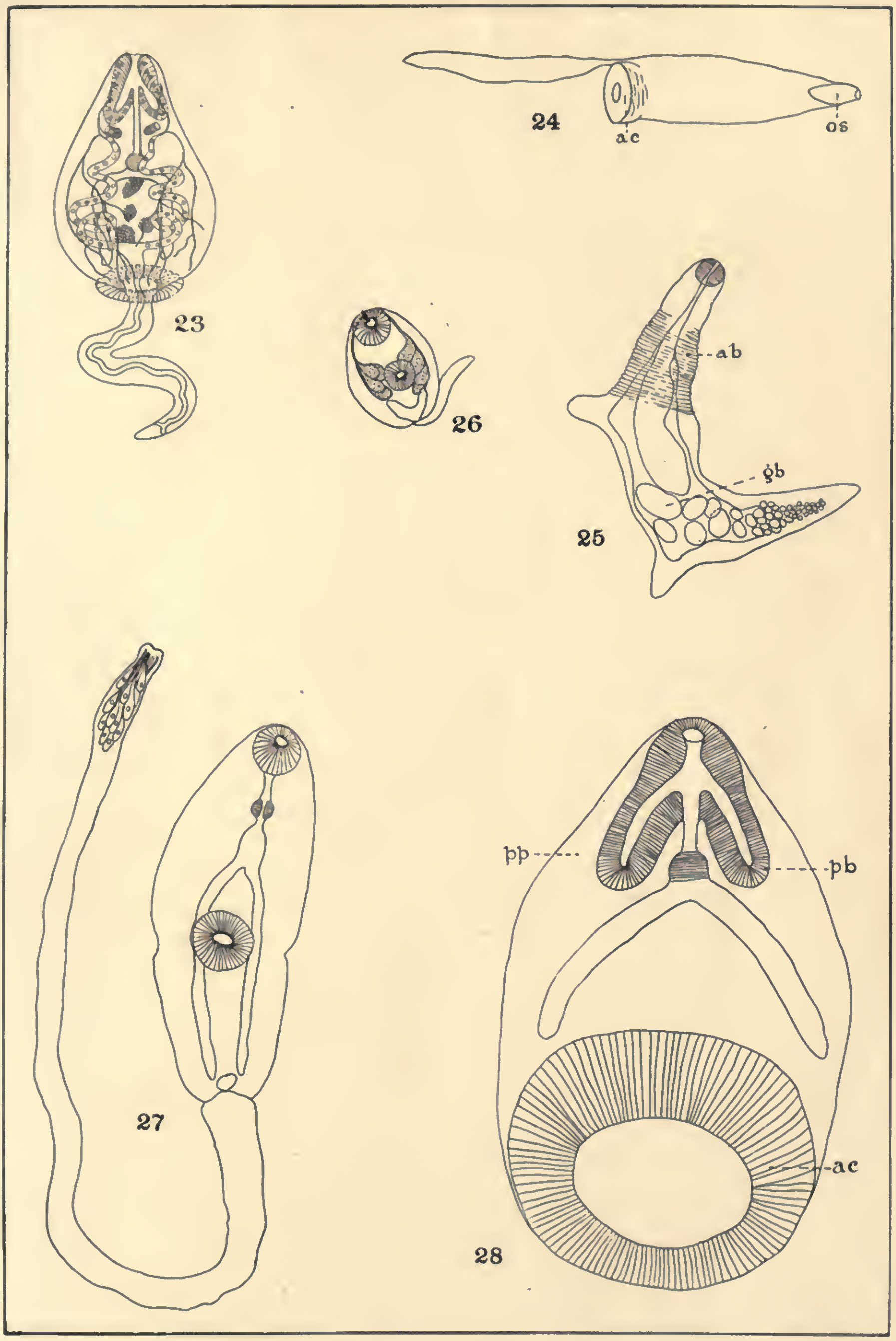

PLATE III

PLATE IV

EXPLANATION OF PLATE

Fig. 29. *Cercaria megalura* before the extrusion of cystogenous material, ventral view. X 195.

Fig. 30. *Cercaria megalura* after the extrusion of cystogenous material, ventral view. X 195.

Fig. 31. Mature redia of *Cercaria megalura*. X 88.

Fig. 32. Cross section of tail of *Cercaria megalura*. X 433.

Fig. 33. Cross section of *Cercaria megalura* before the extrustion of cystogenous material. X 276.

Fig. 34. Cross section of *Cercaria megalura* after the extrusion of cystogenous material. X 276.

Fig. 35. Cross section of immature redia of *Cercaria megalura*. X 433.

Fig. 36. Immature redia of *Cercaria megalura*. X 88.

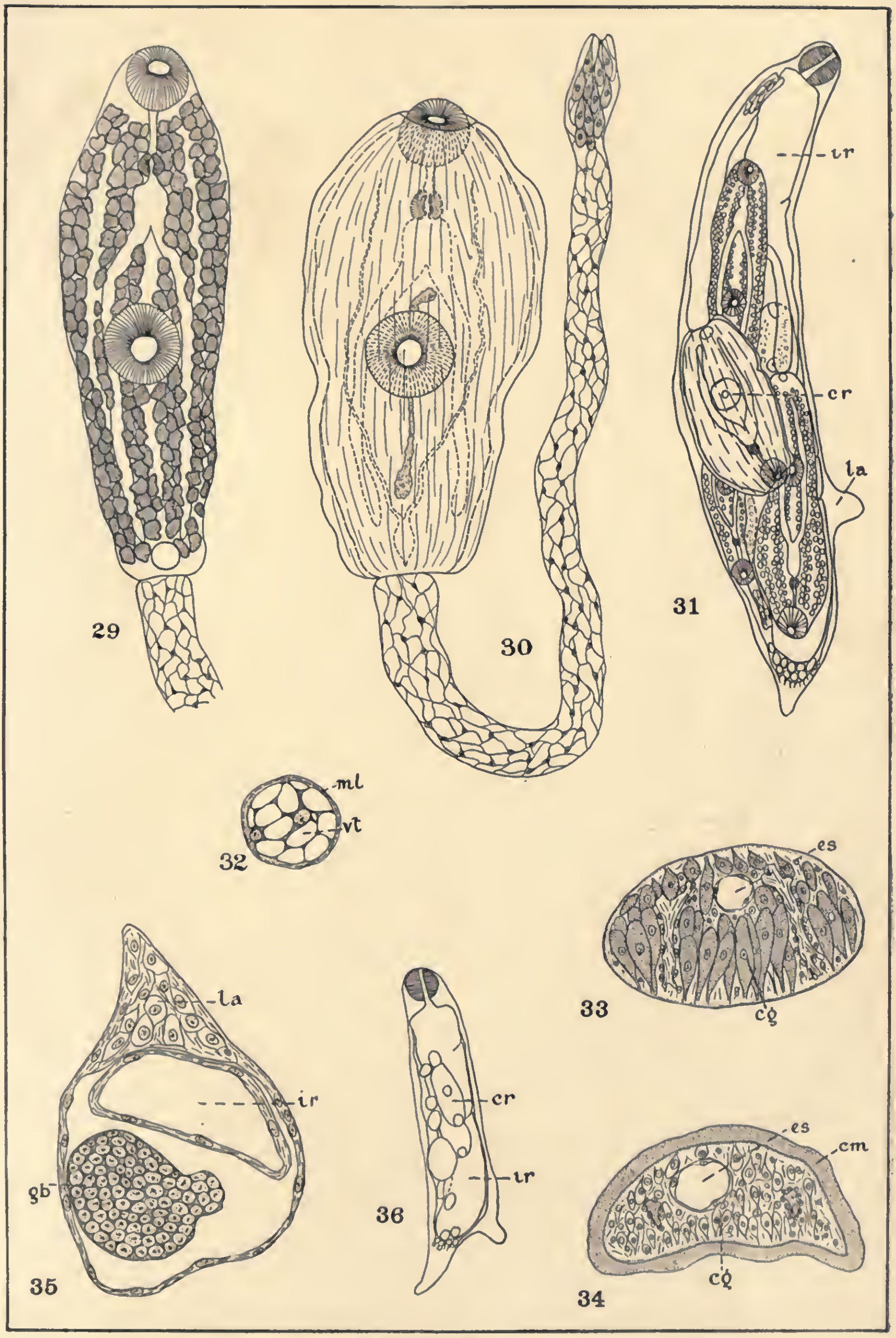

PLATE IV

PLATE V

EXPLANATION OF PLATE

Fig. 37. Mature redia of *Cercaria trivolvis.* X 88.
Fif. 38. Immature redia of *Cercaria trivolvis.* X 88.
Fig. 39. Mature *Cercaria trivolvis,* ventral view. Cystogenous glands not shown. X 195.
Fig. 40. *Cercaria rubra* freed from cyst, ventral view. X 195.
Fig. 41. *Cercaria rubra* inside of cyst. X 195.
Fig. 42. Anterior end of *Cercaria rubra,* dorsal view. X 195.
Fig. 43. *Cercaria reflexae,* ventral view. Cystogenous glands not shown. X 88.

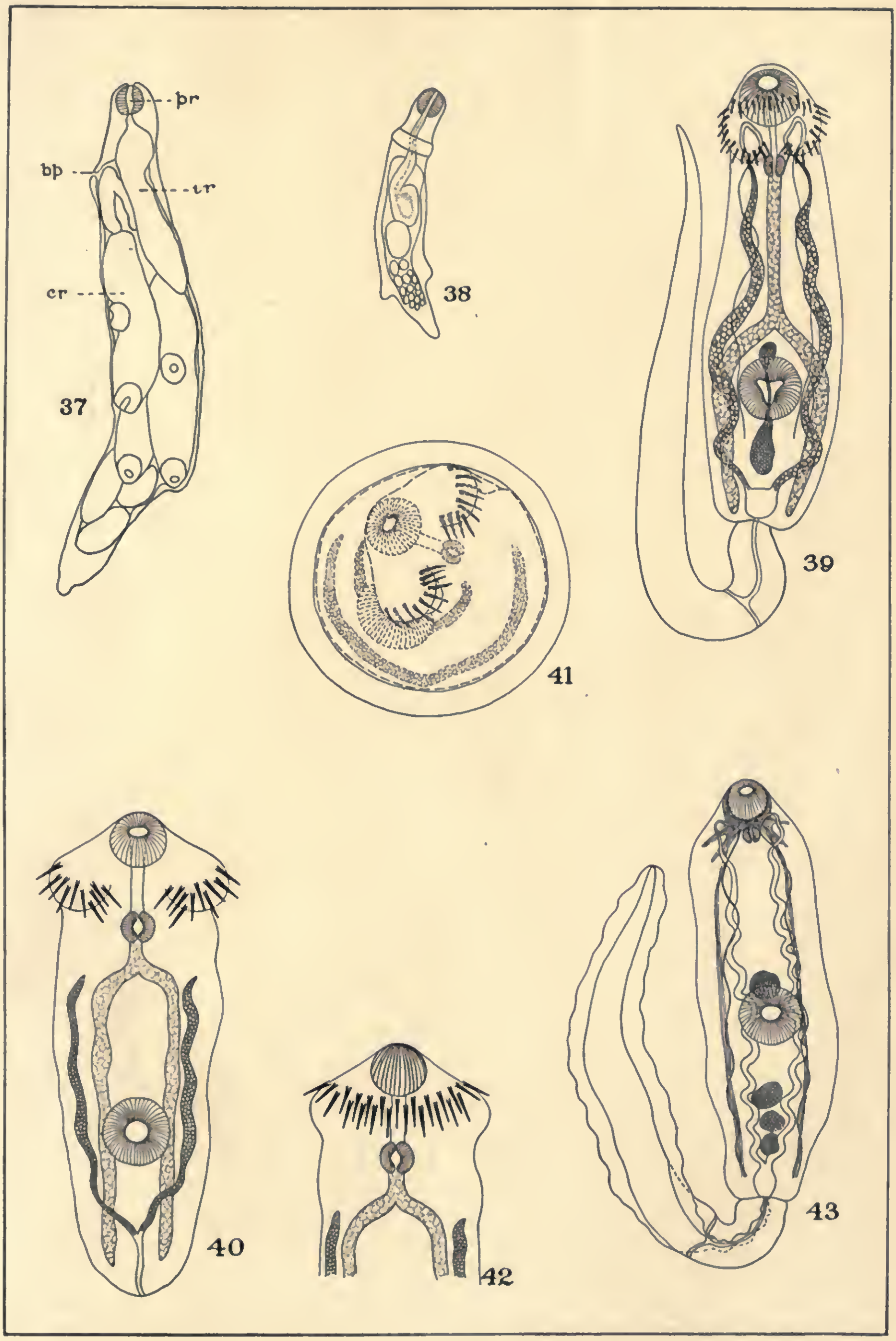

PLATE V

PLATE VI

EXPLANATION OF PLATE

Fig. 44. Immature relia of *Cercaria reflexae.* X 88.
Fig. 45. Mature redia of *Cercaria reflcxae.* X 44.
Fig. 46. Nervous system of immature redia of *Cercaria reflexae.* X 276.
Fig. 47 and 49. Stylet of *Cercaria trigonura,* side view and ventral view. X 433.
Fig. 48 and 50. *Cercaria trigonura,* side view and ventral view. X 195.
Fig. 51. Very immature redia of *Cercaria trigonura.* X 195.
Figs. 52 and 53. Rediae of *Cercaria trigonura,* containing germ balls. X 140.
Fig. 54. Cross section of *Cercaria trigonura* in region of acetabulum. X 433.

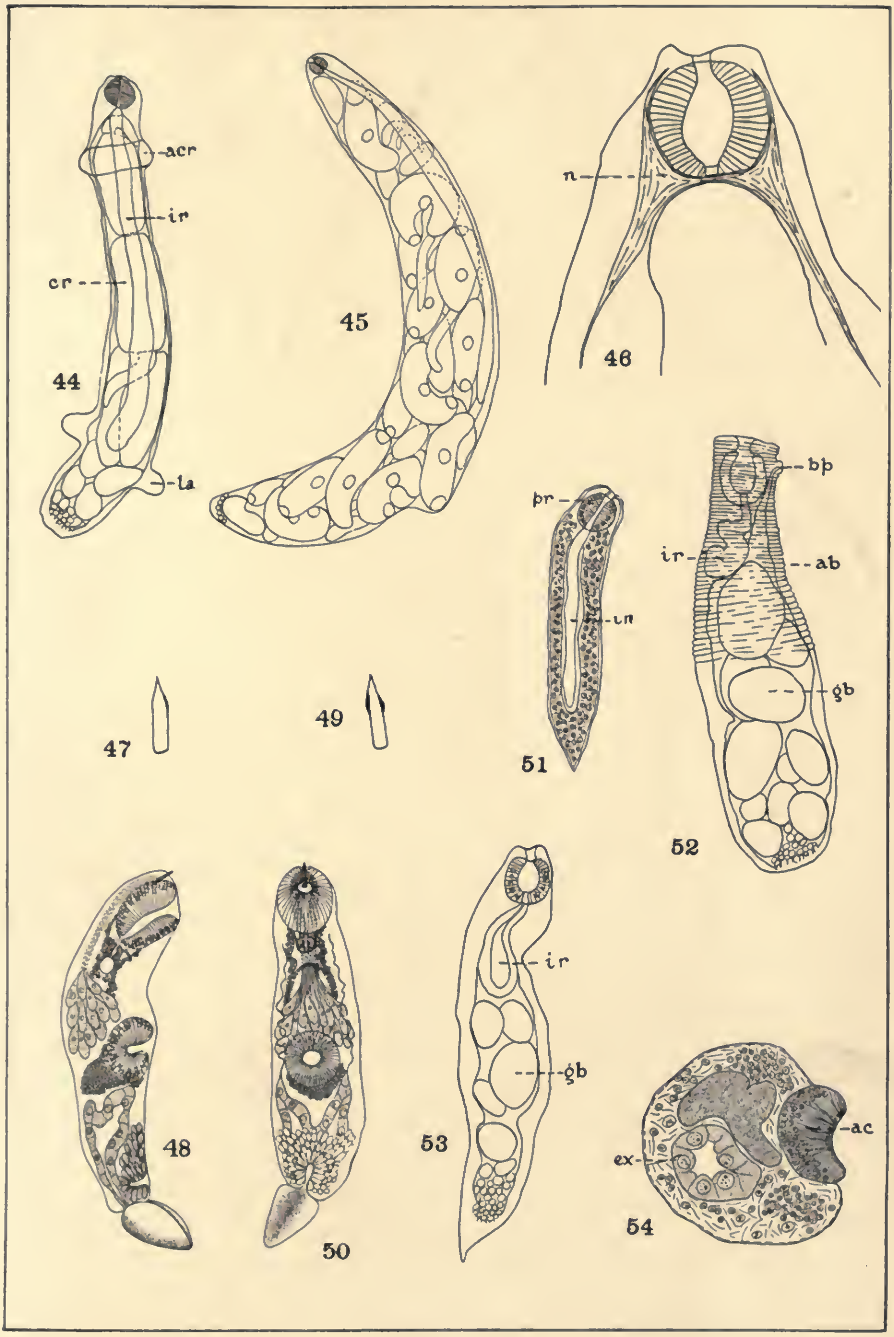
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PLATE VI

PLATE VII

EXPLANATION OF PLATE

Fig. 55. *Cercaria douthitti,* ventral view. X 195.
Fig. 56. Cross section of *Cercaria douthitti* thru eye-spots. X 433.
Fig. 57. Diagram of the excretory system of *Cercaria douthitti* in the region where the tail joins the body. X about 400.
Fig. 58. Cross section of *Cercaria douthitti* thru the acetabulum. X 433.
Figures 59 to 62. Cross sections of *Cercaria douthitti* showing the passage of the ducts of the cephalic glands thru the oral sucker. X 433.
Fig. 63. Section thru a sporocyst of *Cercaria douthitti* while still included in the snail's liver. X 433.
Fig. 64. A portion of a sporocyst of *Cercaria douthitti.* X. 44.
Fig. 65. A portion of a sporocyst of *Cercaria isocotylea.* X 44.
Fig. 66. Sporocyst of *Cercaria isocotylea.* X 44.
Fig. 67. Stylet of *Cercaria isocotylea* from ventral and side view. X 433.
Fig. 68. *Cercaria isocotylea,* ventral view. X 311.

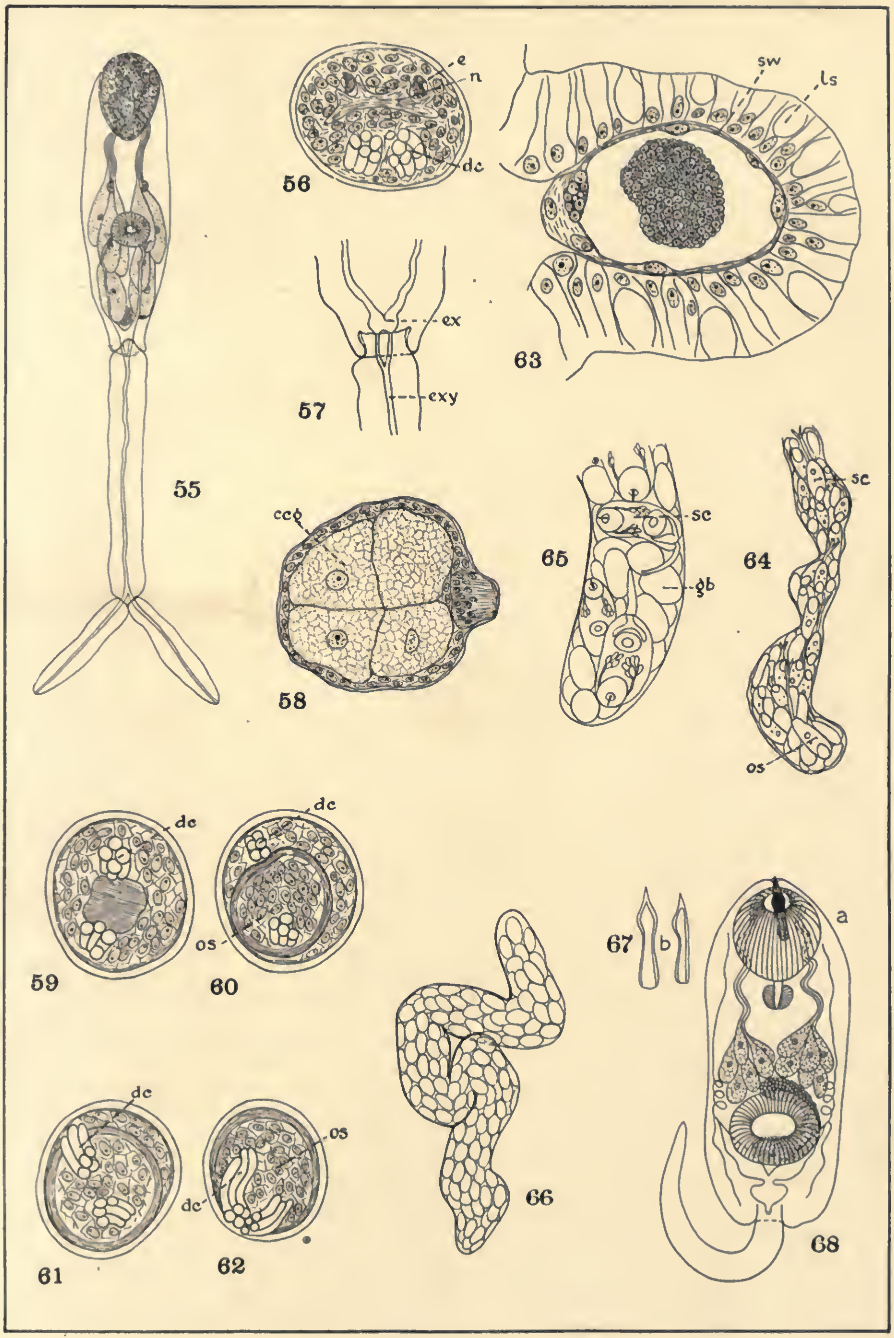
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PLATE VII

PLATE VIII

EXPLANATION OF PLATE

Fig. 69. Stylet of *Cercaria polyadena,* ventral view. X 433.
Fig. 70. *Cercaria polyadena,* ventral view. Cystogenous glands not shown. X311.
Fig. 71. *Cercaria polyadena* in cyst. X 140.
Fig. 72. Sporocyst of *Cercaria brevicaeca.* X 88.
Fig. 73. Stylet of *Cercaria brevicaeca,* ventral view. X 433.
Fig. 74. Free hand drawing of *Cercaria brevicaeca,* ventral view. Cystogenous glands not shown. X about 150.
Fig. 75. Stylet of *Cercaria hemilophura*, side view. X 433.
Fig. 76. *Cercaria hemilophura,* ventral view. Cystogenous glands not shown. X 140.
Fig. 77. A portion of a sporocyst of *Cercaria hemilophura.* X 44.
Fig. 78. *Cercaria hemilophura,* side view. X. 140.
Fig. 79. Stylet of *Cercaria leptacantha,* ventral view. X 433.
Fig. 80. Immature *Cercaria leptacantha,* ventral view. X 433.
Fig. 81. Sporocyst of *Cercaria leptacantha.* X 88.

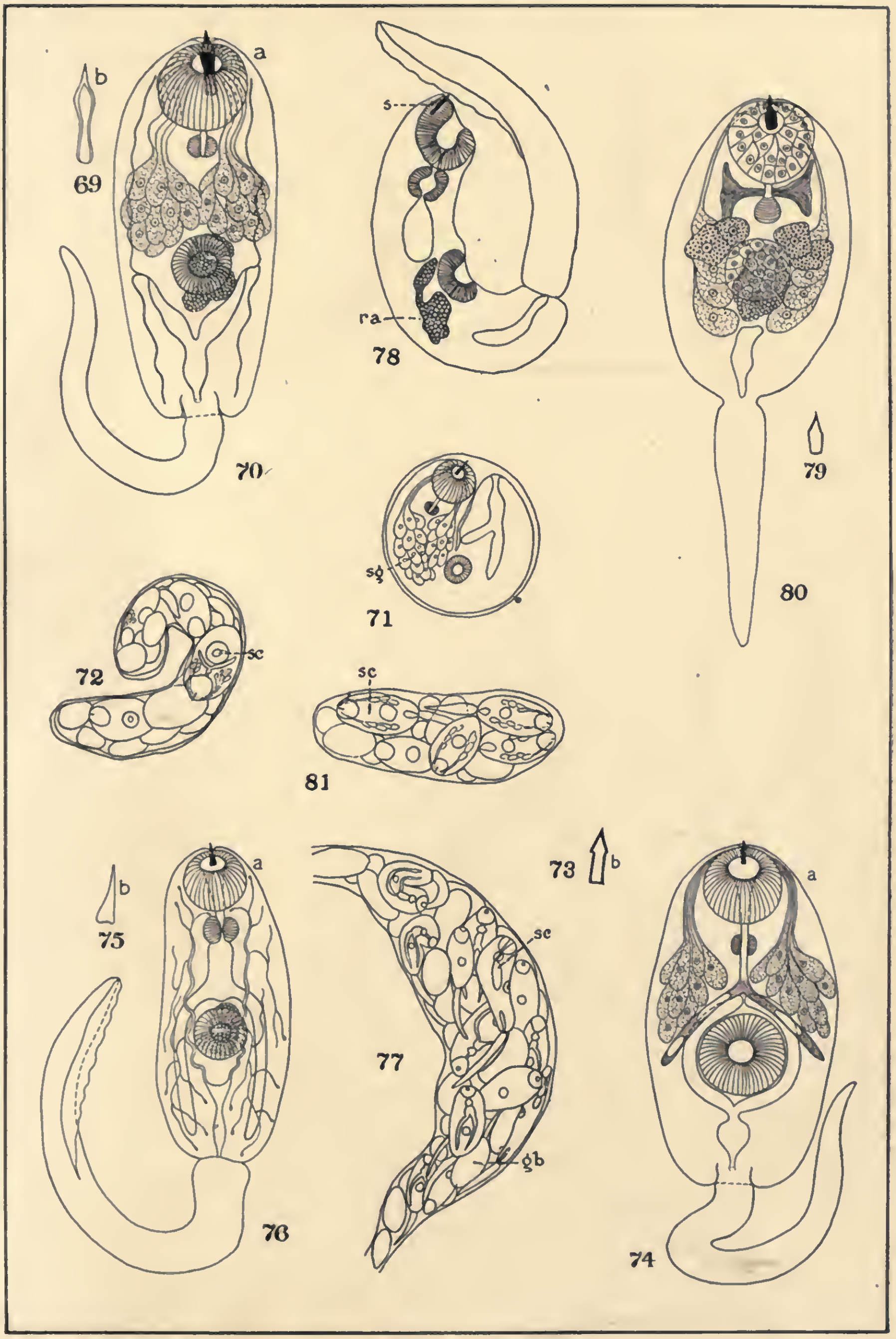

PLATE VIII